Reintroduction and Conservation of the Great Bustard Otis tarda

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Reintroduction and Conservation of the Great Bustard *Otis tarda*

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Image 1: Female Red 28 flying above the release site on Salisbury Plain. This image won 1st prize in the Images of Research competition 2011 at the University of Bath. Photograph by John Burnside.

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Summary

Conservation reintroduction aims to establish an organism into an area from where it has disappeared or was extirpated. Monitoring is essential to identify the factors that underpin successful establishment and persistence of a self-sustaining population. The Great Bustard (*Otis tarda)* is globally threatened and became extinct as a breeding species in the United Kingdom (UK) in 1832. Trial releases began in 2004 to reintroduce the Great Bustard to the UK based on the release of captive-reared chicks transported from a source population in Russia. The aim of this research was to investigate the factors influencing the establishment of a founder population of Great Bustards in the UK. In Chapter 1, I set the context of the reintroduction science and management in the world today and explore the issues surrounding it.

Chapter 2 sets the baseline by which to measure the Great Bustard reintroduction project using the first five years of releases (2004 – 2008). Estimating vital rates and modelling population growth, I show that low recruitment to the founder population is a limitation for establishment.

Chapters 3 and 4 investigate post-release survival and dispersal, both important variables in population establishment. By modelling individual post-release survival I show that earlier date of release can improve survival and could be used to improve recruitment. Conversely, post-release dispersal had mixed implication for the management of the reintroduced population. Surviving Great Bustards incorporated the release site into their annual range and as their breeding site. However, the birds had traversed large areas reducing our ability to monitor and control the environment of individuals.

In Chapter 5, the research focus moves from the reintroduction project to an examination of the impact of disturbance and conspecific attraction (presence of conspecifics positively influences the movement of individuals) in habitat selection in a small extant population of Great Bustards. I show that the spatial distribution of display sites is influenced by anthropogenic disturbance; however, the number of males attending the display sites is influenced by the abundance of female conspecifics. The management implications of this result are that the attraction to conspecifics is an important factor in habitat selection.

Finally, in Chapter 6, I discuss project limitations, potential interventions and identify future areas of research.

Image 2. Male Great Bustard patrolling a lek in Saratov, Russian Federation.. Photograph by John Burnside.

Chapter 1: Introduction

Robert J. Burnside

Conservation Science: Reintroduction - Restoring Biodiversity and Natural Heritage

There is a growing urgency to respond to the global loss of biodiversity (Strategic Plan for Biodiversity 2011-2020). With increasing conservation efforts there have been concomitant calls for conservation action to be based on evidence (Sutherland *et al.* 2004). Even though extinction is an everyday biological process which on geological timescales is matched by speciation, the current rate of extinction is higher than the background rate verging on a sixth mass extinction (Barnosky *et al.* 2011). It is estimated that one quarter of all vertebrates could become extinct in the next century (Baillie *et al.* 2010). Furthermore, only 4% of known described species have had their conservation status assessed. Of this, 31.6% have been classified as being threatened with global extinction (IUCN 2012). Global population decline and range reduction are a prerequisite to extinction and consequently form two of the key criteria for quantifying extinction risk (IUCN 2012). However, species do not decline uniformly across their range but by the loss of discreet populations (Hughes *et al.* 1997). Disappearance of populations is usually known as local extinction and ultimately leads to further isolation and fragmentation of remaining populations (Ceballos & Ehrlich 2002). Hence, extinctions (or intentional extirpations) can vary in spatial scale from local, to regional or even global. Conservation efforts mainly take place at a population level and generally attempt to reverse population decline or increase small populations (Caughley & Gunn 1996). However, even with intensive conservation work on extant populations, reversing local extinctions is unlikely to occur if the historical areas are isolated or if an organism's life history traits reduce its recolonisation potential (IUCN 1998). Therefore human intervention in the form of translocation, *"moving organisms from one area to free release in another"*, may prove a more effective or at least a quicker way of restoring populations and ranges (IUCN 1998).

Translocations have occurred for a variety of reasons; for example, stocking game species (Griffith *et al.* 1989). However, the proliferation in its use for conservation purposes has emerged as an increasing trend of the last 30 – 40 years (Seddon *et al.* 2007). For conservation purposes, translocations can be split into, but not limited to, four types: reintroduction; translocation; supplementation-and introductions (IUCN 1998). Reintroduction is *"the intentional movement of an organism into a part of its native range from which it has disappeared or become extirpated in historical times"* (IUCN 1998). The objectives of a reintroduction are to re-establish a self-sustaining population which needs little or no further intervention (Griffith et al. 1989; Seddon 1999).

Species from all higher taxa have been part of reintroductions from invertebrates to mammals (Table 1). There has been much debate over how useful reintroductions are as a conservation tool. By its nature reintroductions are often treated on a case by case basis, and consequently, there are many examples of case studies of different reintroduction outcomes. The first reintroduction on record is that of the capercaillie *Tetrao urogallus* which became extinct in

Scotland in the 18th century and was reintroduced from a Scandinavian population in the 1830s. The population still exists today although it has been declining since the 1970s and currently at risk of a second extinction (Moss 2001).There are many examples of exceptional successes which have brought species back from the brink of extinction. The pink pigeon *Columba mayeri* of Mauritius was reduced to *ca.*10 individuals in 1990 and the 2011 population is *ca.* 400 birds. This dramatic recovery was achieved through, captive-breeding, reintroduction and intensive management. Strategies used included, predator control, establishing additional meta-populations, cross-fostering and supplementary feeding (Jones & Merton 2012). New Zealand has multiple examples of bird species being saved through translocation and reintroduction. The North Island saddleback *Philesturnus carunculatus*, a wattlebird, was reduced to *ca.* 500 in 1964 and in 2011 the population was estimated at > 10, 000 birds. These are distributed across 13 islands and two mainland populations. This was successful due to the movement of the birds onto invasive predator-free islands and the provision of artificial nests (Jones & Merton 2012).

Table 1. Trends in numbers of animal species that are the focus of known reintroduction projects from 1900. Taken from Seddon et al. (2007).

Taxon	**1900–1992**	**By 1998**	**By 2005**
Invertebrates	2	19	65
Fish	9	11	20
Reptile & amphibians	22	42	94
Birds	54	69	138
Mammals	39	77	172
Total	126	218	489
References	Beck 1994*	Stanley Price & Soorae 2003	Seddon *et al.* 2005

**Includes only the reintroduction of captive-born animals and is therefore likely to be an underestimate of all animal reintroduction projects*.

Conversely, there are many examples of reintroductions that have failed. Ruffell *et al.* (2009) attempted to review reintroduction and translocation attempts of bats but the documentation of projects was poor and they found no examples of successful projects. Six attempts to reintroduce threatened wallabies (Marsupialia: Macropodoidea) in mainland Australia have also failed due to the high rate of predation by exotic predators (Short *et al.* 1992).Additionally, there are more complicated examples of how otherwise successful projects can encounter problems such as that seen with the capercaillie (see above). For example, the reintroduction of the Arabian oryx *Oryx leucoryx* to Oman is one of the pioneering projects often cited as a case study on how successful a reintroduction can be. Following the extinction of the species in the wild in1972, several releases

occurred in the 1980s. By 1990 the founder population reached 100 individuals and continued to grow, reaching 400 in 1996. At this point, the initiation of poaching caused a rapid decline in the restored population to just 138 animals (28 female, 110 male) within 3 years and by 1999 the population was then no longer deemed viable (Spalton *et al.* 1999).

In another example, the reintroduction of the red kite *Milvus milvus* throughout southern England and parts of Wales was a major success (Evans et al. 1999). This is in contrast to efforts in Scotland where the species has failed to thrive due to secondary poisoning as the result of the use of bait poison laid for other predators (Smart et al. 2010).

Table 2. Collection of the outcomes from different systematic reviews into translocations covering all taxa.

Publication	**Purpose**	**Taxa**	**n**	**Successful %**	**Fail %**	**Uncertain %**
(Griffith *et al.* 1989)	Translocations of endangered species	Mammals and birds	198	44	56	
(Dodd & Seigel 1991)	Reintroduction & translocations	Amphibians and reptiles	26	19	23	58
(Fischer & Lindenmayer 2000)	Reintroduction (conservation + other purposes)	All taxa	180	26	27	47
(Singer *et al.* 2000)	Reintroduction	Bighorn sheep *Ovis canadensis*	100	41	30	29
(Matson *et al.* 2004)	Reintroduction	Black-faced impala *Aepyceros melampus*	21	62	38	
(Hayward *et al.* 2007)	Reintroduction	Large carnivores	28	42.8	14.2	42.8
(Godefroid *et al.* 2011)	Reintroduction	Plants	249	Survival: 52 Flowering: 19 Fruiting: 16	48 81 84	
(White Jnr *et al.* 2012)	Reintroduction	Parrots	47	55	45	
(Soorae 2008, 2010, 2011)	Reintroduction	All taxa	184	Highly Successful: 19 Successful: 36 Partially Successful: 40	4	

With the impressive successes of individual cases shown above there has been a sense that ALL reintroductions are successful and this is often the public perception (Caughley & Gunn 1996; Dodd & Seigel 1991). This has led to an inflated sense of success whereas empirical reviews have

been less supportive (Table 2). Table 2 gives an example of the outcomes from systematic reviews of reintroductions which have actually shown that many translocations and reintroductions result in failure. Additionally, the estimated success rates are probably overestimates as the failures are often not reported (Beck et al. 1994; Dodd & Seigel 1991; Fischer & Lindenmayer 2000; Griffith et al. 1989; Wolf et al. 1996).

Several conclusions can be drawn from these reviews: 1) often reintroduction projects do not have comparable measures of success (Fischer & Lindenmayer 2000); 2) they often do not have adequate information to evaluate the outcome of the project (Fischer & Lindenmayer 2000; Godefroid et al. 2011); 3) there is a bias in publications towards successful projects. For example, Godefroid *et al.* (2011) found a 33% higher survival rate of plants in the scientific literature than those reported in surveys, indicating that successful projects are more likely to get published. And 4) most reintroductions fail to establish a population that persists (Table 2). Nonetheless, reintroduction is becoming an increasingly used tool for restoration as indicated by its increased prevalence in the literature (Bajomi et al. 2010; Fischer & Lindenmayer 2000; Seddon et al. 2007).

Understandably, a growing interest has emerged on what the specific elements are that make a reintroduction successful. Systematic reviews (Table 2) have identified various important factors correlated with success. These can be grouped into three broad categories in order of importance: habitat, management and organism life history.

Habitat: all reviews found that selecting the appropriate habitat for release site and target establishment area, as well as the quality of habitat, are important predictors of success (Griffith et al. 1989; Wolf et al. 1998). The presence of predators and removal of the cause of decline can also be classified as part of habitat quality (Fischer & Lindenmayer 2000). Attempts to reintroduce plants have been more successful within protected areas (Godefroid et al. 2011). Furthermore, locating the release areas closer to the core of the species range rather than the periphery has been shown to lead to increased success (Griffith et al. 1989; Wolf et al. 1998).

Management: across all reviews considered here, the number of organisms released has been found to be an important predictor of success (Beck et al. 1994; Fisher & Owens 2004; Godefroid et al. 2011; Griffith et al. 1989). In the choice of wild versus captive source populations, it has been shown that projects using wild-reared animals have a better outcome (Fisher & Owens 2004). Supportive measures, such as pre-release acclimatisation, have had mixed outcomes, working for some species and not others (Fisher & Owens 2004).

Life history: reproductive traits, such as early breeding, large clutches and herbivory, were initially positively correlated with success (Griffith et al. 1989). However, these variables did not remain significant on reanalysis with phylogenetic constraints (Wolf et al. 1998). There is surprisingly little evidence of life history traits influencing reintroduction outcome in these reviews. A lack of

evidence has been similarly found for establishment in biological invasions (Fisher & Owens 2004). However, a comparison of introduced and reintroduced bird species finds that introduced species are less threatened, have larger ranges and earlier ages at maturity, than reintroduced species (Blackburn & Cassey 2004).

The common important themes between all of these reviews on predictors of success can be summed up as follows: 1) The choice of release site with suitable high quality habitat is important (habitat quality should include a measure of competitors and predators). 2) Success is positively correlated with the number of individuals released, and 3) reintroducing organism within their range, i.e. climate matching, can improve success. Even though we have developed some general trends for improving success in the field of reintroduction, such as the IUCN guidelines, it is clear that many reintroductions fail (Table 2). The actual causes of failure are rarely identified or measured because of the lack of long-term post-release monitoring (Seddon et al. 2007).

Why is it important to study reintroductions?

Conservation reintroductions are an important conservation tool and have a variety of benefits. These include restoring natural heritage, restoring ecosystem function, restoring distribution and restoring meta-population structure (Armstrong & Seddon 2008). Given the substantial costs involved in a reintroduction project using finite conservation funds and the ethical issues of releasing animals that are doomed to die, there is a need to establish an evidence-base upon which we can improve the outcomes of reintroductions. Although monitoring itself is not management, it allows for the collection of data upon which to base decisions involving interventions and the deployment of management strategies. It is now generally accepted that monitoring is an integral part of any reintroduction. However, the next challenge for monitoring is to establish standardised protocols across different reintroductions. This in turn makes the synthesis of common themes across projects more accessible for meta-analysis and comparison (Fischer & Lindenmayer 2000; IUCN 1998; Sutherland et al. 2010).

The development of the discipline of "*Reintroduction Biology"* is the result of the acknowledgement that there was a need for a rigorous scientific approach to the improve reintroduction and translocation outcomes (Armstrong & Seddon 2008). Consequently, more theory and structure has developed. Additionally, knowledge gained may be transferrable to other types of translocations and supplementations. Reintroduction techniques will also be applied to future translocations that are envisaged as having a role to play in mitigating the effects of climate change on vulnerable species (Seddon 2010).

The development of theory and hypotheses in reintroduction biology has drawn on the analogous fields of biological invasions, non-conservation introductions and restoration ecology (Blackburn & Cassey 2004; Lipsey & Child 2007). Further theory has been drawn from more

traditional conservation biology, particularly hypotheses associated with the small population paradigm and the declining population paradigm (Caughley 1994). However, the advancement of the theory-based hypothesis testing is still limited in reintroductions as there is often conflict the between the scientific and management objectives (Caughley & Gunn 1996). It is clear that reintroduction biology must integrate science and management objectives (Seddon et al. 2012).

The fundamental stages of the reintroduction process (at its simplest) can be thought of as containing two elements: establishment and persistence (Seddon *et al.* 2007). Establishment is defined as the *"survival and successful breeding by founder individuals and their offspring"* (Seddon et al. 2012). Persistence is defined as *"the likelihood of population decline or extinction over some population specific time"* (Seddon et al. 2012). Establishment can further be seen to consist of two phases - a lag phase and a growth phase. The founder population will remain small for a time until conditions are right for rapid population growth until density dependent regulation begins.

"Establishment is a prerequisite for, but not a guarantee of, population persistence" (Seddon *et al.* 2012). Although there are examples of reintroduced populations encountering difficulty after successful establishment, see earlier examples of Arabian oryx and capercaillie, failures are most likely to occur during the establishment phase (Grey-Ross et al. 2009; Parish & Sotherton 2007; Short et al. 1992). Consequently, understanding the factors influencing the founder population is of importance for reintroductions as a whole and is the primary focus of this research.

Reintroduction establishment phase

Understanding establishment is fundamental to improving outcomes of reintroductions and a key area of research (Armstrong & Seddon 2008). The theories of propagule pressure and small population paradigm relate directly to establishment probability. Propagule pressure was developed from research on biological invasion and suggests that more individuals, or pressure, during an invasion event increases the probability that some individuals will survive and persist (Colautti et al. 2006; Lockwood et al. 2005). This is the converse of the small population paradigm which predicts when a population consists of few individuals, there is a greater chance of extinction due to random fates to individuals, i.e. demographic stochasticity (Caughley 1994). Additionally, the small population paradigm also incorporates Allee effects, the reduction of vital rates at low population numbers or density (Stephens et al. 1999). Allee effects may reduce establishment probability through low probability of finding mates, missing social cues, or reduced predator vigilance (Armstrong & Reynolds 2012). These theories both suggest that larger founder populations, or remnant populations, will have a greater probability of establishing. The results of the systematic reviews discussed above agree with the theory set out here. Therefore, releasing enough individuals to establish a founder population and understanding the factors that influence this are a priority.

The number of individuals that form the founder population is influenced by three factors: the number of released, post-release survival and dispersal away from the target release area. The former factor is often difficult to manipulate when working with rare or threatened species because of limitations in stock numbers. However, post-release survival and dispersal can both be influenced through pre and post-release management which is a key area of focus for reintroduction biology (Seddon et al. 2007), and for modelling population trajectories (Armstrong & Reynolds 2012).

Chapter 2 explores the factors influencing the process of establishment in reintroduction and uses modelling to explore how variation the factors will influence the outcome.

Post-release Survival

Mortality of organisms after release serves to reduce the number of released individuals recruiting into the founder population thereby slowing grow, or potentially causing extinction. Firstly, it is important to make a distinction between survival and post-release survival. Survival is an estimate of the probability of a normal individual surviving through a pre-defined period of time, usually annually. However, released organisms often experience a period of elevated mortality after release when individuals acclimate to their new environment. The period of lower survival is generally finite and probability of surviving through this period can be referred to *post-release survival* (Hamilton *et al.* 2010). If they survive through this period they then become part of, i.e. recruited into, the founder population. Armstrong & Reynolds (2012) termed these *post-release effects* and dispersal can also be affected during this period (see below).

Low post-release survival has been exhibited by a wide variety of released organisms. For example, crested coots *Fulica cristata* experienced a third of the mortality that occurred in the first month after release (Tavecchia et al. 2009). Plants have even been found to have increased high mortality rates after release (Godefroid et al. 2011). Very low post-release survival has lead to the failure of many projects. For example, captive-breed oribi *Ourebia ourebi*, an African antelope, had seven of ten individuals die in the first two months after release prompting a halt to further releases (Grey-Ross et al. 2009). Grey partridge *Perdix perdix* only had 10 % of 520 released survive from autumn to the following spring. This resulted in the authors opposing the use of captive-reared partridge in any further releases unless measures were taken to tackle the problem (Parish & Sotherton 2007).

The most common stated cause of mortality among vertebrates is predation, however this is likely a proximate cause, whereas ultimately it is due to released individuals lacking the correct predator avoidance skills, or having maladaptive behaviours developed in captivity. More recent theory is focusing on the effects of accumulated effects of stress before and after release as a cause of post-release effects (Dickens et al. 2010; Teixeira et al. 2007). Alternatively, in the case of

oceanic islands, the animals may not have an evolved responses to introduced predators and the only way to mitigate this is through eradication of predators (Jones & Merton 2012; Short et al. 1992).

Dispersal

Dispersal in relation to reintroductions can be defined as any movement away from the release area either temporarily or permanently (Le Gouar et al. 2012). It is important to quantify the rates of dispersal as this will have consequences for the number of individuals recruiting into the founder population and reintroduction management. Dispersal of released organisms can undermine efforts to establish a reintroduced population in three ways. Firstly, long distance movements away from the target establishment area effectively removes individuals from the population (Le Gouar et al. 2012). Dispersal by reintroduced griffon vulture *Gyps fulvus* was the cause of establishment failure during multiple releases after controlling for mortality (Le Gouar et al. 2008). Second, release sites and target areas are generally managed specifically to improve the habitat for the released species, whereas dispersing animals are likely to end up in unmanaged areas. For example, 32% of reintroduced New Zealand black stilts *Himantopus novaezelandiae* dispersed from the target area with 15% of them settling in areas with no predator control (van Heezik et al. 2009). Lastly, long distance movements will decrease the ability for monitoring the released individuals (Hardman & Moro 2006). Understanding the causal drivers in movement will allow for manipulation through pre and post-release management (van Heezik et al. 2009).

Pre and post-release management of post-release mortality and dispersal

Post-release survival and dispersal can both be manipulated through pre and post-release management. There are many examples of strategies that can be used to help with acclimatisation of released animals into their new environment. Examples of pre-release management include puppet-rearing birds, foster-rearing, using wild individuals rather than captive-reared, predator-awareness training and social group composition. Post-release management can include soft-release confinement, hard release, predator free enclosures, supplementary feeding, varying release date and season, releasing different age groups, using decoys to attract conspecifics, cutting flight feathers and predator control.

Many techniques have entered "*conservation management lore*" but upon inspection through reviews, the hard evidence rarely supports them and manipulations may not have the desired effect. The displacement of red foxes *Vulpes vulpes* and feral cats *Felis domesticus* away from release areas of houbara bustard *Chlamydotis undulata macqueenii* slowed the temporal and changed the spatial distribution of predation but did not change the overall rate (Combreau & Smith 1998). Experimental testing of soft and hard release on two species of hare-wallaby, mala *Lagorchestes hirsutus* and merrnine *Lagostrophus fasciatus,* showed there was no difference in the

survival or dispersal rates between the two techniques, although soft release takes greater effort and resources (Hardman & Moro 2006).

Experimentally testing, or *a posterior* modelling, the different techniques can yield important insights into their efficacy. However, valid assessment requires effective pre and post-release monitoring of the released individuals over an appropriate time period as some effects may only emerge over the long-term. For example, short-term monitoring of New Zealand kaki *Himantopus novaezelandiae* showed initial differences in release site fidelity when releasing juveniles or subadults, but after two years equal proportions had returned. Ultimately the release strategies were not different but the effect would not have been seen with short-term monitoring (van Heezik et al. 2009)

There are still large gaps in knowledge about the processes and behaviours regulating the survival and dispersal of released organisms. For example, the disparity between survival of wild-bred and captive bred animals shows that the captive-reared animals often lack the behaviours that allow wild-bred counterparts to have higher survival rates (Evans et al. 2009; Nicoll et al. 2004). There is currently little understanding of how and what the infant animals will learn from parental input and hence it has been poorly replicated in captivity (Griffin & Blumstein 2000; van Heezik et al. 1999). Understanding these processes is one of the ten key questions in the future of reintroduction biology (Armstrong & Seddon 2008).

Chapters 3 and 4 present the results of modelling the influence of pre and post-release management on survival and dispersal and the influence it will have on the management of reintroduction.

Habitat selection & conspecific attraction

Conspecific attraction can confound traditional interpretations of habitat selection and therefore it is relevant to conservation management (Danchin *et al.* 2004). Habitat selection is the process whereby individual animals assess a site for structure and resources important to their fitness and make a decision to occupy the habitat or not based on that assessment (Morris 2003). Whereas, conspecific attraction theory suggests that rather that assessing the habitat directly, individuals use the presence or abundance of conspecifics as an indicator of habitat quality (Muller et al. 1997).

The role of conspecific attraction in shaping species distribution can be particularly important for managing the reintroduction of social species (Mihoub et al. 2011). Understanding the habitat preferences of a target reintroduction species is fundamental for the selection of release sites (Osborne & Seddon Philip 2012). The establishment process will be complicated if released individuals are selecting habitat based on the presence or abundance of conspecifics rather than the actual habitat quality. Long-distance dispersal initiated by conspecific attraction resulted in failure to establish griffon vultures *Gyps fulvus* and caribou *Rangifer tarandus* (Bergerud & Mercer 1989;

Le Gouar et al. 2008). Further, when used in habitat selection by small populations, conspecific attraction can have a run-away effect on reducing population growth through behaviourally mediated Allee effects (Kokko & Sutherland 2001; Mihoub et al. 2009; Stephens et al. 1999). If sub-optimal habitat is selected it can lead to an *"ecological trap"*, whereby individuals continue to select the poor habitat because conspecifics are present.

Understanding the role of conspecific attraction in a species' behaviour is an important management consideration. In Chapter 5, I investigate the role of conspecific attraction versus habitat in breeding site attendance in a small population of Great Bustards.

The Great Bustard *Otis tarda*

The Great Bustard *Otis tarda* is one member of the 26 species in the Family: Otididae. It holds the status as the bird with the largest sexual size dimorphism and is one of the heaviest flying birds (mean adult body mass, females: 7 kg; males: 14 kg) (Alonso et al. 2009; Székely et al. 2007). It is a gregarious species that occupies same-sex flocks. Its breeding behaviour can be described as a lek mating system; however, it does not meet all the classical definitions of a lekking species and is often described as having an exploded lek system. Males congregate on traditional leks spread over large areas during spring, in an effort to display and attract females. Females are ground-nesting and nest on or near the lekking area. The female takes sole care of hatchlings and has long parental care of up to one year after hatching. Sexual maturity is usually reached at 2 (females) and 4 (males) years old (Morales & Martin 2003). It is well adapted to the low intensity agriculture and showing a preference for this over natural steppe grassland (Gewalt 1959; Morales & Martin 2002). However, modern farming methods and intensification increasingly cause habitat loss for Great Bustards. Other threats to the species have been hunting, predation of its ground nests, collision with power lines and anthropogenic disturbance (Birdlife International 2012)

Global conservation status

The Great Bustard has been classified as Vulnerable on the IUCN Red List since 1994 and has a current world population estimate is 43,514 - 51,227 individuals (IUCN 2012; Palacin & Alonso 2008). Great Bustards underwent a range expansion in the 18th century during an increase of agriculture and deforestation throughout Europe. In more recent times it has experienced steep declines in population size and range (Morales & Martin 2002). For example, in Germany the population collapsed from 4000 to 50 individuals in a 50 years period (Langgemach 2008). Similarly, the Hungarian population decreased from 3,400 to 1,100 individuals between in 1980 and 1996 (Collar 1985; Farago 1996). Range reductions have also been reported in Russia, Spain and Portugal during the past three decades (Alonso et al. 2005; Pinto et al. 2005). Most notably there have been historical national extinctions in the UK, France, Italy, Greece, Yugoslavia and Poland (Palacin & Alonso 2008).

UK Great Bustard reintroduction

The Great Bustard became extinct as a breeding species in the United Kingdom (UK) in 1832 - possibly through a combination of factors such as: hunting and egg collection; increase in the use of the plough during agriculture advances; and an historical period of cooler climate (Osborne 2002).

The possibility of natural recolonisation is unlikely within a foreseeable timeframe due to the distance and isolation of the UK from extant populations. Therefore, reintroduction represents the most viable option of establishing the species in the UK. The Great Bustard Reintroduction project followed IUCN Reintroduction Specialist Group guidelines (IUCN 1998) and undertook a feasibility study (Osborne 2002).

Great Bustards have responded poorly to captive-breeding attempts and therefore the only viable option was to transport chicks from a donor population (Collar & Goriup 1980; Martin 1996). A source population was identified in Russia where there is a long established practice of rescuing eggs from agricultural destruction, *ca*. 30 years (A. Khrustov, pers. comm.). Chicks reared in Russia could then be transported to the UK and released onto a release site in Salisbury Plain (Fig 1.). Salisbury Plain was the last known breeding area for Great Bustards in the UK prior to national extinction. In 2003, a licence was issued by Department of the Environment, Food and Rural Affairs (DEFRA) to enable Great Bustard Group to undertake a 10 year period of trial releases. The Great Bustard is long lived (20 – 30 years) with delayed maturity and low productivity (Martinez 2008; Morales & Martin 2003). The release stock was also limited to rescued eggs so and release numbers would be restricted. Therefore we expect to measure output over a long period of time and accordingly this comparatively short research focuses on the factors that influence the early stage of establishment.

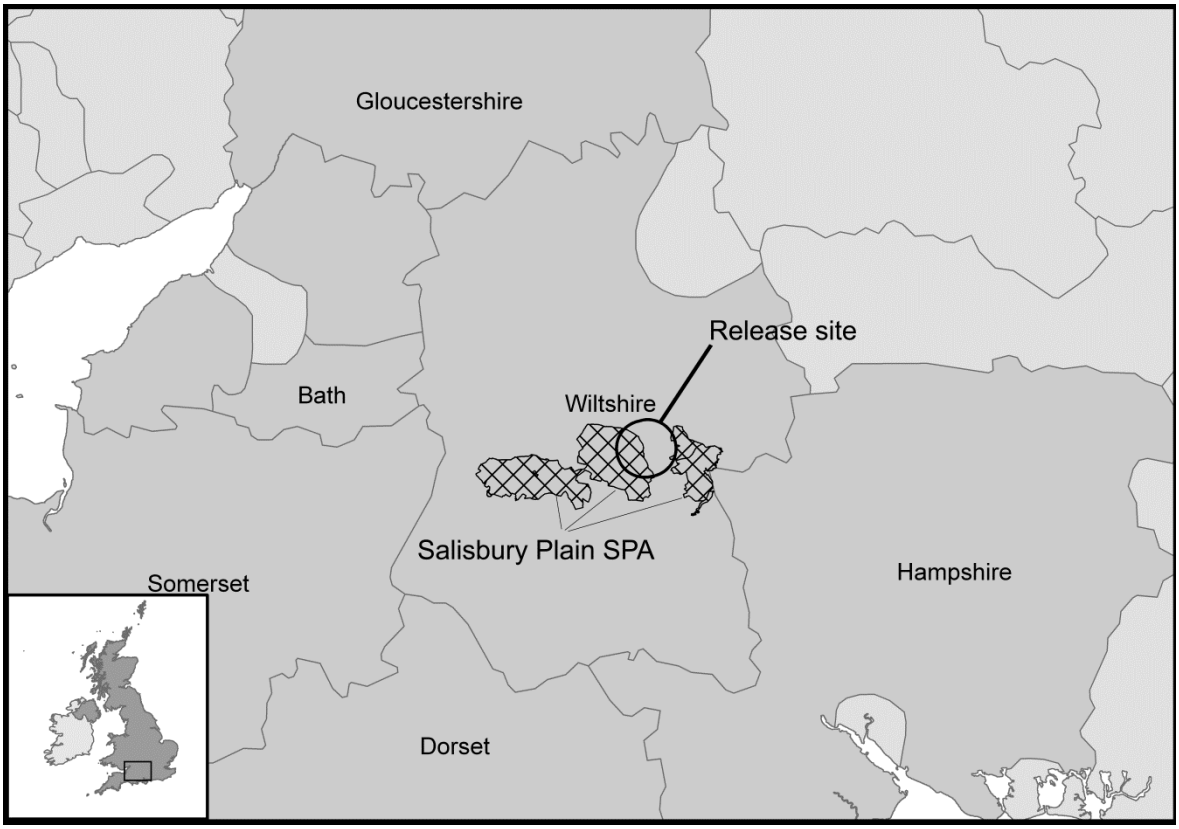

Figure 1. Location of the UK Great Bustard reintroduction release site on Salisbury Plain special protected area (SPA).

PhD Objectives

I had multiple objectives for the PhD research to fill gaps in our knowledge about the issues affecting Great Bustard reintroduction and conservation. There were gaps in our knowledge of the vital rates of captive-reared Great Bustards and bustards in the UK. Also, it was unknown what parameters would have a limiting effect on establishing a founder population, therefore modelling was the best approach to make population projections for understanding the establishment a founder population (Chapter 2). As mentioned earlier, post-release survival and dispersal influence reintroduction outcome. Therefore, quantifying and understanding how release methodology and individual characteristics are important for project management (Chapters 3 & 4). This allows for an evidence-based approach to assess and make decisions about management. In the final data Chapter (5), I investigate the roles of disturbance and conspecific attraction of display site choice and attendance of Great Bustards using observational data from a small population in Hungary. The size of the study population reflects the target size of the envisaged reintroduced UK population. The geographical extent of this population is similar to the UK release area and the population processes in this population may be a good model for which to explore future ecology of the UK

population. Finally, in Chapter 6, I discuss the consequences of the results for the UK Great Bustard population and reintroductions and future directions for research.

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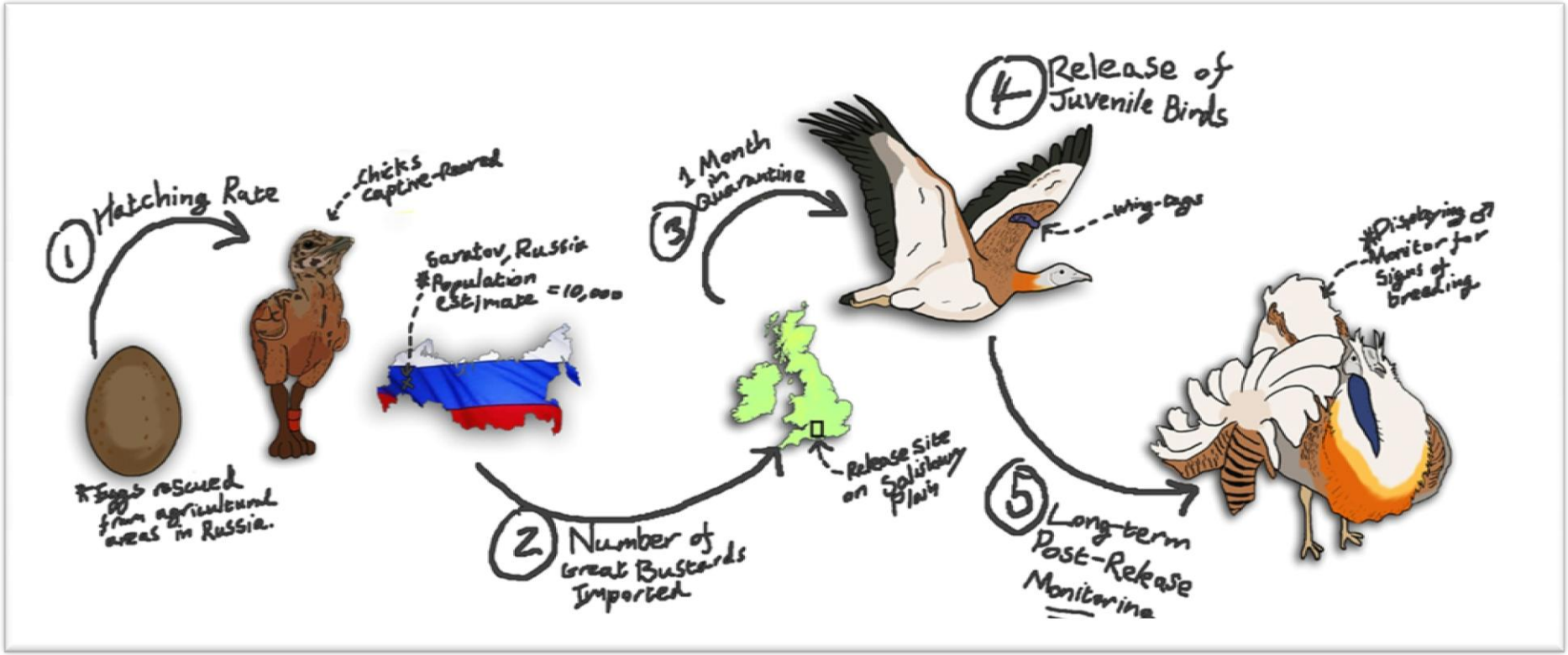

Image 3. Illustration of the reintroduction methodology used to reintroduce Great Bustards to the UK by the Great Bustard Group. Illustrations by John Burnside.

Chapter 2: The UK great bustard *Otis tarda* reintroduction trial: a 5-year progress report

Robert J. Burnside, Ian Carter, Alasdair Dawes, David Waters Leigh Lock, Paul Goriup and Tamás Székely

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Author's contributions

RJB: statistical analysis, manuscript preparation
IC: Manuscript improvement
AD: Data collection, manuscript improvement
DW: Manuscript improvement
LL: Manuscript improvement
PG: Manuscript improvement
TS: Manuscript improvement

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Image 4. Collisions with fences and power lines are a problem for many bustard species. I found this Great Bustard feather wedged in a barbed wire fence while searching for the individual. Photograph by John Burnside.

Chapter 3: Refining reintroduction release methods: modelling post-release survival of captive-reared Great Bustards.

Robert J. Burnside, Alasdair Dawes, Kate Ashbrook, David Waters, Ian Carter and Leigh Lock

Manuscript

Author's contributions

RJB: statistical analysis, manuscript preparation
AD: Data collection, manuscript improvement
KA: Manuscript improvement
DW: Manuscript improvement
IC: Manuscript improvement
LL: Manuscript improvement

Abstract

High post-release mortality during reintroduction programmes can reduce the probability of population establishment. The use of monitoring data to model individual survival can help to develop evidence-based methods for improving survival. Here we use seven years of post-release monitoring data to investigate the influence of release methodology on post-release survival of captive-reared Great Bustards *Otis tarda* released as part of a trial reintroduction in the UK. Using Burnham live resighting and dead recovery survival models, estimated monthly survival during the six month critical period after release was low (65.7 %), although there was some evidence of improvement during this period. We found that survival rates for juvenile birds were higher for birds released in late August (77 %) and decreased for birds released later in the autumn, falling to 46% for October releases. Age at release and release date were correlated and we could not conclusively separate the two effects. Therefore, environmental conditions related to seasonality at the time of release and the period of time spent in captivity may both influence mortality. The long period of vulnerability is suggestive of a lack of appropriate behavioural responses potentially due to the processes of captive-rearing and release methodology. We did not find support for influences of release group size or monitoring attachments on survival. Based on this evidence, we recommend that bustards should be released as soon as possible after their typical age of fledging. These results will help inform release methodology that may increase the survival of captive-reared birds in future.

Keywords: Burnham, great bustard, monitoring, release, reintroduction, survival, UK

Introduction

High post-release mortality can reduce the probability of establishing founder populations during reintroduction programmes (Armstrong & Seddon 2008; Seddon et al. 2007; Teixeira et al. 2007). Reintroduction projects often use captive-bred or captive-reared animals, and aim to establish a self-sustaining population in an area from which they have become extinct (IUCN 1998). Although there have been many notable successes (Jones & Merton 2012), it is estimated that only 11% to 62 % of reintroductions succeed overall (Beck et al. 1994; Fischer & Lindenmayer 2000; Griffith et al. 1989; Wolf et al. 1996). High post-release mortality can lead to failure even when the habitat in the release area is suitable (Moseby et al. 2011; Parish & Sotherton 2007). It reduces recruitment rates to a founder population, in turn increasing the number of individuals needed to establish a population and the time required to undertake the releases (Burnside et al. 2012). Given the resources needed to implement and monitor a reintroduction, the continued development of methods to increase survival of released animals is essential to improve reintroduction outcomes (Fischer & Lindenmayer 2000; Seddon et al. 2007).

Post-release mortality of captive-reared animals is characterised by a critical period of time after release when individuals are more vulnerable to mortality than wild-born conspecifics (Armstrong & Reynolds 2012; Tavecchia et al. 2009). The length of this critical period of vulnerability varies between species and has been documented for a variety of plants, invertebrates, mammals and birds (Biggins et al. 2011; Godefroid et al. 2011; Mitchell et al. 2011; Nicholls & Pullin 2000). The increased risk of mortality experienced by captive-reared animals can be attributed to two causes, 1) in the time immediately following release, individuals may experience stress due to the captive rearing and release processes (Dickens et al. 2010; Teixeira et al. 2007); and 2) the absence of the correct behavioural responses as a result of captive-rearing can increase vulnerability to predation (Parish & Sotherton 2007; Wallace 2000).

Understanding the influence of release methods, and social and individual characteristics on post-release survival can help improve reintroduction outcomes (Mitchell et al. 2011; Rouco et al. 2010). Insight into such factors is beneficial because they can be manipulated to increase survival, however, they are often species specific (Hardman & Moro 2006). Release group size has been found to be important in some species (Bernardo et al. 2011) and not in others (Buner & Schaub 2008). Age at release and time in captivity can be considered synonymous as captive-reared animals spend their life in captivity until release. Both are considered to be important factors in reintroduction release methods demonstrating variably beneficial and negative effects between species with increasing time (Mitchell et al. 2011; Rouco et al. 2010) vs (Black et al. 1997; Green et al. 2005; Jones & Merton 2012). Lastly, the timing of release can be important due to seasonal effects (Bernardo et al. 2011; Bright & Morris 1994; Tavecchia et al. 2009).

The Great Bustard *Otis tarda* is currently categorised by the IUCN as Vulnerable (www.iucn.org) due to rapid population declines and local extinctions across much of Europe during the 20th

century (Palacin & Alonso 2008). The Great Bustard became extinct as a breeding species in the UK in the 1830s (Osborne 2005). In 2003, a 10 year government license was issued for a trial release project to assess the feasibility of a full reintroduction and annual releases of captive-reared Great Bustards started in 2004 (Osborne 2002). After five years of releases, high post-release mortality was recognised as a key factor limiting the chances of the project achieving its aims. Specifically, the first six months post-release was identified as a period of increased vulnerability to mortality (Burnside et al. 2012). Previous studies found no difference in survival rates between the sexes of released individuals and sex is therefore not considered further in this study (Burnside et al. 2012).

Using live resighting and dead recovery data from seven years of releases and capture-mark-recapture, we model post-release survival of reintroduced Great Bustards to investigate patterns of survival during the critical period of six months following release. We had two objectives in this study; the first was to explore survival and changes in survival during the first six months after release by finding the most parsimonious model when considering different detectabilities in resighting and recovery probabilities; and secondly, to use the most parsimonious survival model(s) to assess the effect and relative importance of release date, age at release, release group size and release year on survival of released Great Bustards. A further objective was to assess if any cost to survival was incurred by carrying transmitters used for monitoring. Our aim was to develop release methodologies with a view to improving post-release survival in the captive-reared Great Bustard.

Methods

Species and study area

The Great Bustard is a large (mean adult body mass, females: 7 kg; males: 14 kg), and slow maturing bird. In the wild, chicks fledge (sufficiently developed to fly) between 30-35 days but remain with the mother for 6 to 12 months (Morales & Martin 2003). Great Bustards have been released each autumn at a site located on Salisbury Plain, South-West England from 2004 to 2010. The release area, rearing and import of chicks from Russia are described elsewhere (Burnside et al. 2012; Osborne 2005).

Release

From 2004 to 2010, 147 Great Bustard chicks were transported *c*. 3,500 km to the UK. Fifteen birds died prior to release and ten birds were either confined to the release pen, held back to allow for further development or recovery, or were unfit for release. A total of 122 captive-reared Great Bustards were released onto Salisbury Plain release site in the UK.

Imported birds are required to complete a statutory 30 day quarantine period before release. The release site has an open-topped release pen that is surrounded by an electrified 2 m high fence designed to exclude red foxes *Vulpes vuples* and badgers *Meles meles*; this area was extended from

3.5 ha to 7 ha in 2008. Limited predator control for red foxes was done on the release site outside the release pen.

The reintroduction release methodology has varied between years, but ultimately concludes with release cohorts being placed into the release pen. Some birds were released directly into the release pen, while others were held in a small netted pen within the larger release pen for approximately one week prior to being let out. Release dates were variable between years (Table 1), and were often constrained by the date of importing chicks from Russia and the quarantine requirement. Releases took place from late August to late October (range 52 days), and the total number of birds released each year varied between four and 32 individuals (Table 1). Release group sizes varied between one and 17 individuals (Table 1). The mean age at release was 99 days (range 58 – 145 days), whereas the mean range in age within release groups was 22 days (range 4 – 46 days).

Post-release monitoring

Each bird had two identical colour-coded wing-tags comprised of an individual identifying number on a coloured background, denoting release year. In addition, four different tracking devices were used to help monitor released birds: 1) harness-mounted backpack Argos/GPS enabled LC4™ platform transmitter terminals (PTT; Microwave Telemetry Inc., Columbia, USA), 105 gram for males and 40 g units for females; 2) harness-mounted backpack Biotrack TW-3 72 g VHF transmitters ; 3) necklace-mounted Biotrack TW-3 15.5 g VHF transmitters, which can only be used on females due to continuing male neck growth; and 4) tail-mounted Biotrack TW-3 12.2 g VHF transmitters (Table 1). Backpack harnesses were fitted using a standard mounting procedure with straps passed over the front of the birds, crossing on the chest and returning through the scapular area. In 2004, elastic strapping braided along the length was used whereas in all subsequent years fixed-width elastic strapping was used (Alonso 2008).

For 2004, only monitoring data was available for dead recoveries whereas all other years have monitoring records for resighting and recoveries. Since the project resources have changed through the years, we expect the resighting monitoring effort to vary between the years.

Monitoring was not carried out in systematic intervals, but rather as a near-continuous presence at the release site throughout the year. The area monitored covered approximately 2 km in radius from the release pen and we defined this as the survey area. This limitation in search radius was due to the layout of roads and restrictions on movement in the adjacent military areas. The release pen is adjacent to a hide and project office from where it can be observed with telescope. The release area beyond the pen was searched by driving on pre-existing tracks and searching for birds using telescopes from vantage points.

Mortalities were reported via carcass, wing-tag and transmitter recovery. For the modelling approach adopted, released individuals that were recaptured due to injury were considered dead on that date as they were effectively removed from the population.

Table 1. Number of captive-reared Great Bustards released in the UK from 2004 to 2010. The number surviving to six months is contained within parentheses. The release date; the release technique used (H = not contained in netted pen, S = contained in netted pen); and the type of monitoring attachment used. See Methods for explanation.

Year	Julian Release day	Release technique	No Transmitter		Backpack		Tail-mount		Necklace	Total
			Male	Female	Male	Female	Male	Female	Female	
2004	270	S	1 (1)	1 (1)	9* (0)	9* (0)	-	-	-	20 (2)
2005	237	H	4 (0)	2 (0)	-	-	8 (2)	2 (0)	2 (1)	18 (3)
	249	H	-	-	-	-	4 (1)	8 (1)	2 (1)	14 (3)
2006	289	H	-	-	-	-	3	-	6 (1)	9 (1)
2007	268	H	-	-	3 (2)	1 (0)	-	-	-	4 (2)
2008	268	H	1 (0)	12 (1)	2 (0)	2 (0)	-	-	-	17 (1)
2009	256	H	-	-	2 (0)	3 (1)	-	-	-	5 (1)
	260	S	7 (0)	3 (0)	-	-	-	-	-	10 (0)
	274	H	1 (0)	-	-	-	-	-	-	1 (0)
	286	H	-	2 (0)	-	-	-	-	-	2 (0)
2010	251	H	3 (1)	-	2 (0)	-	-	-	-	5 (1)
	266	H	-	2 (0)	-	4 (1)	-	-	-	6 (1)
	275	S	1 (0)	-	5 (0)	-	-	-	-	6 (0)
	282	S	-	1 (0)	-	4 (0)	-	-	-	5 (0)

*Backpack VHF, all other backpacks are satellite PTTs.

Survival analysis

We chose to use capture-mark-recapture (CMR) modelling because it gives the ability to control for different detectabilities due to time and monitoring devices. We used Burnham's combined live encounters and dead recoveries analysis to model post-release survival as multiple data sources can improve reliability of models (Burnham 1993).

Resightings beyond the monitored area were not included to meet the assumptions of CMR modelling, however, dead recoveries could be included from within and beyond the monitored area (Burnham 1993).

The Burnham model consists of four probability parameters, survival (*S*), resighting (*p*), recovery (*r*), and site fidelity (*F*). The data from all releases were pooled. Resighting and recovery histories from 122 released Great Bustards were constructed from monitoring data collected between August 2004 and July 2011. We wanted to understand on a fine temporal scale the individual variation in survival through the 6-month critical period after release. As the data were not collected in a predefined systematic fashion suited to CMR assumptions we chose to use a restricted dataset and demark the temporal scale according to the assumptions that resighting period is short relative to the mortality period (Lebreton et al. 1992). Therefore we chose half-month units to achieve the appropriate resolution, with four days for resighting and 11 days with no resightings. Mortality recoveries can occur throughout the entire sampling occasion. This resulted in 11 resighting and 12 recovery occasions. Resighting probability was fixed at zero for birds released in 2004.

Fidelity is defined as the probability of remaining in the monitoring area (Burnham 1993). *F* is not estimable when recoveries are made within the study area (White & Burnham 1999). In this study, not all dead individuals were recovered or last seen within the release site and therefore fixing $F = 1$ would not be valid. Therefore we estimated *F* directly by calculating the proportion of birds either recovered dead or that had their last resighting > 2 km from the release pen. Seventeen of the 122 individuals were in this category. We took the 11^{th} root of 86.07 % to find the fidelity rate per resighting interval and fixed $F = 98.89$ % for all models except the global model.

We used the R *v*.12 (R Development Core Team 2007) package RMark *v*. 2.6 (Laake & Rexstad 2008) to construct and compare models run in program MARK (White & Burnham 1999). The logit link was used in all modelling.

Covariates

Time (S_{time}) was defined in normal CMR fashion as 12 occasions in discrete levels representing time after release.

Release methodology was assessed with Julian release date ($S_{release.date}$; Table 1), and age at release ($S_{release.age}$). The latter two variables were significantly correlated (Fig. 1, Spearman's rank correlation $rho = 0.686$, $p < 0.005$) and so they were modelled individually to understand which

best fits the data. Additionally, we derived a z-score measure of relative age at release ($S_{relative.age}$). This was calculated as the difference in individual age and the mean age of a release group ÷ the standard deviation of the group.

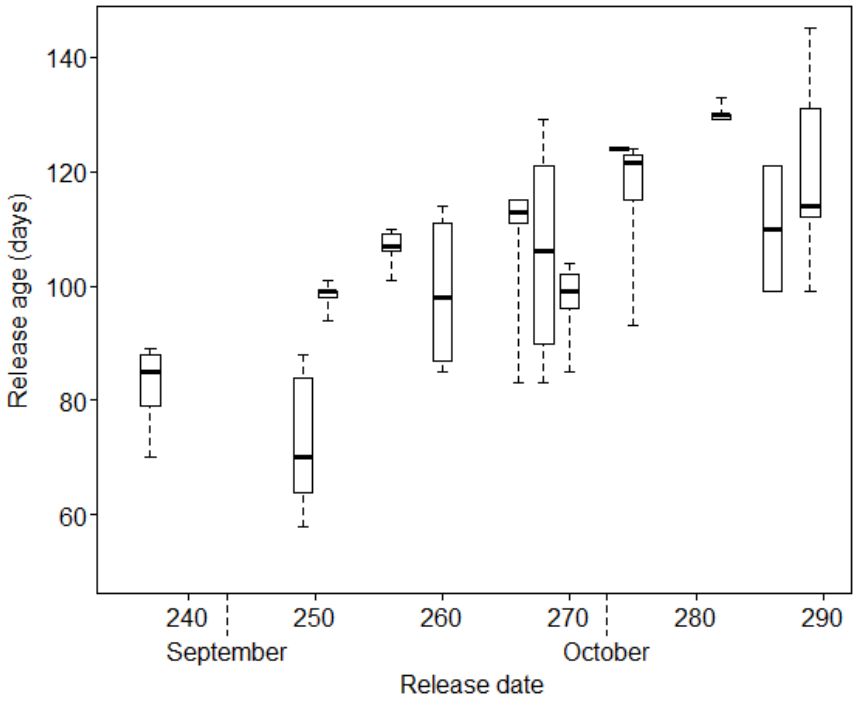

Fig. 1. Boxplots of age at release versus Julian release date for captive-reared Great Bustards released in the UK (n = 122 birds). The thick black lines within boxes represent the median, boxes are interquartile range and bars are the full range.

Great Bustards are gregarious and may acquire behaviours socially; therefore, we added a variable to investigate the influence of release group size on survival ($S_{cohort.size}$). Release year (S_{year}) was tested to determine if post-release survival rates varied between years.

A five-level factor ($S_{attachment}$) was used for transmitter attachment type, described above, with an additional fifth group for individuals with no transmitters. Attachment mass can be important and is often a limiting factor in transmitter choice when studying birds. However, due to unrecorded masses for 13 birds, we chose not to include the ratio of transmitter to bird mass in modelling. Indications from the available data are that the weight of transmitters was not important. For birds with mass records, the mean mass at release was 4.4 kg for males (range 2.6 – 5.4 kg) and 2.9 kg for females (range 1.9 - 4.2 kg). Therefore, all fitted transmitters were < 3 % of total body mass which is less than the usually accepted guideline of < 5 % (Burger & Shaffer 2008).

Survival models

We constructed two sets of models to test hypotheses about survival and release methodology. First, a fully time-dependent global model ($S_{time} \cdot p_{time} \cdot r_{time} \cdot F_{time}$) was taken as a starting model and no age structure was included in the model because only juveniles were considered. We then constructed a set of 25 models to find the most parsimonious survival model when considering influence of time after release (S_{time}) on survival and further resighting and recovery probabilities. Our *a priori* hypotheses were that resighting and recovery probabilities could be influenced by time after release ($p_{time;}\, r_{time}$), attachment type ($p_{attachment;}\, r_{attachment}$), release year ($p_{year;}\, r_{year}$), and additive interactions between attachment type and time ($p_{attachment + time;}\, r_{attachment + time}$) and year and time ($p_{year + time;}\, r_{year + time}$). Every combination between *r* and *p* was tested including constant rates ($p_{c;}\, r_c$).

Secondly, using the most parsimonious survival model(s), we tested six different hypotheses of the influence of the release covariates influence of individual survival.

Model fit and selection

We use information theory to compare and select the best model upon which to make inference (Burnham & Anderson 2002). We can rank the different hypotheses according to how well the respective model fit the data. We assessed fit and overdispersion of the global model ($S_{time} \cdot p_{time} \cdot r_{time} \cdot F_{time}$) to the data by running 1000 replicates of the standard goodness-of-fit bootstrap test from program MARK (White & Burnham 1999). We used the bootstrap method on the Burnham model as other methods cannot estimate variance inflation factor (ĉ) from resighting-recovery data (Cooch & White 2011). The observed deviance indicated overdispersion and ĉ was estimated as 1.26 and all models were adjusted. Therefore we used quasi-corrected Akaike's information criterion (QAICc) to select the best supported model from the candidate set. Models were considered different if the difference in QAICc (ΔQAICc) was > 2 (Burnham & Anderson 2002). Evidence ratios of relative model support were calculated as, larger model weight ÷ smaller model weight. We report monthly survival estimates unless otherwise stated and standard errors were calculated using the deltamethod (Laake & Rexstad 2008).

Results

Post-release survival, resighting and recovery

Of the 25 models selected to investigate post-release survival, model 1 ($S_c \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$) received all the support (QAICc weight = 1.00) and a ΔQAICc > 14 from the second model. The model can be interpreted as follows, survival rate was constant during intervals; resighting probability varied and interacted between years and time after release ($p_{year + time}$); and recovery probability was influenced by the transmitter type ($r_{attachment}$).

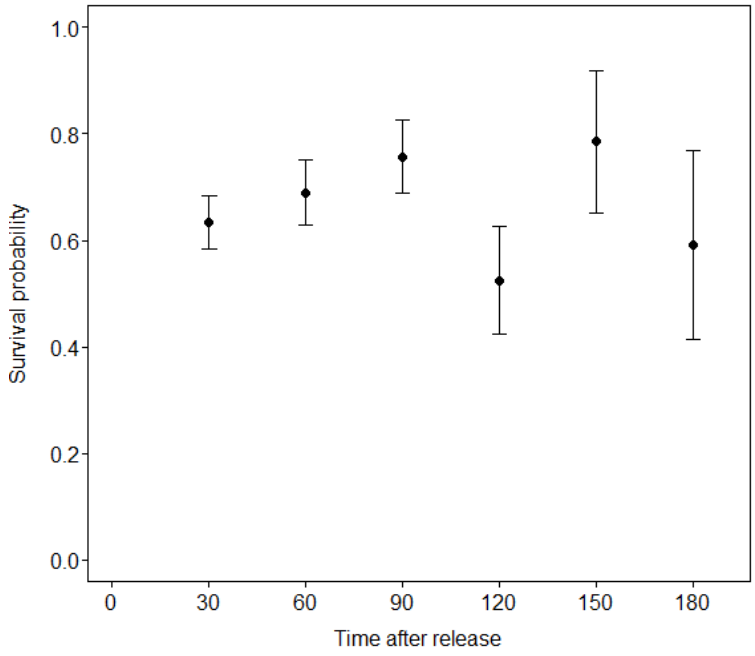

Fig. 2. Survival probabilities of captive-reared Great Bustards released in the UK for the first six months after release. Survival estimates are from model 2, Table 2. Standard errors shown were calculated using deltamethod.

As estimated from model 1, mortality was high with a monthly survival probability during the first six months after release estimated as 65.7 % (SE ± 1.78 %). Therefore, the estimated probability of surviving to the end of this period was 10.0 % (SE ± 1.78 %) which is comparable to, but an underestimation of, the number of birds known to be alive at the end of this period: 15 alive from 122 released (12.2 %). Collision (with fences or power lines) and predation were the main causes of mortality accounting for 21 and 16 individuals, respectively. Exact cause of death could not be established for 37 confirmed mortalities due to desiccation of the carcass, or only tags being recovered.

Table 2. Survival probability models for captive-reared great bustards in the UK during a critical six month period post-release. Only the top four models and the global model shown from 25 models. Models are ordered according to quasi-corrected Akaike's information criterion (QAICc). Models are Burnham live resighting and dead recovery models and are denoted as follows: post-release survival (*S*), resighting (*p*) and recovery (*r*) probability and release site fidelity (*F*) in captive-reared great bustards. See methods for explanation of variables. The best model reads as, survival rate was constant between intervals, resighting rates varied between years and time after release, while recovery rates were different between attachments. All models were adjusted with a variance inflation factor, $\hat{c} = 1.26$. The logit-link was used in all models.

No.	Model	No. parameters	QAICc	ΔQAICc	QAICc weights	QDeviance
1.	$S_c \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	23	790.38	0.00	1.00	444.17
2.	$S_{time} \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	34	805.01	14.63	0.00	432.71
3.	$S_c \cdot p_{year + time} \cdot r_{attachment + time} \cdot F_{0.98}$	34	806.93	16.55	0.00	434.63
4.	$S_c \cdot p_{year + time} \cdot r_{year} \cdot F_{0.98}$	25	809.43	19.05	0.00	458.60
5.	$S_{time} \cdot p_{time} \cdot r_{time} \cdot F_{time}$	46	987.03	198.9	0.00	575.34

The probability of recovering a backpack VHF and PTT were estimated as 96.6 % (SE ± 8.0 %) and 99.5 % (SE ± 4.0 %), respectively. Only one individual from the former two groups had an unconfirmed fate, whereas the other groups had a total of 28 birds with unconfirmed fates. The probability of recovery from tail-mounted and necklace transmitters was 65.9 % (SE ± 10.2 %), and 55.9 % (SE ± 16.9 %), respectively, and the probability of recovering an individual with no transmitter was lowest at 43.1 % (SE ± 7.9 %). These estimates are not likely to be influenced by wing-tag loss since only one bird was known to have lost both wing-tags during the study.

There was evidence of improvement in survival probabilities after release (Fig. 2, model 2, Table 2) although this was off-set by decreases during the fourth and six month. Time was not included in further modelling because it received no support compared to the most parsimonious model, with a difference of > 14 QAICc.

Table 3. The influence of release date, age at release, rainfall and release cohort size on post-release survival (*S*) of captive-reared Great Bustards. See methods for explanation of variables. Models are ordered according to quasi-corrected Akaike's information criterion (QAICc) and all model fits were adjusted with a variance inflation factor, ĉ = 1.26. The logit-link was used in all models. See legend in Table 2. All models have a $\cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$ structure except model 5 which was the global model. Models 1 and 5 shown for comparison.

No.	Model	No. parameters	QAICc	ΔQAICc	QAICc weights	QDeviance
6.	$S_{release.date} \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	24	784.57	0.00	0.79	732.95
7.	$S_{release.age} \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	24	788.87	4.29	0.09	737.24
8.	$S_{cohort.size} \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	24	790.20	5.63	0.05	738.58
1.	$S_c \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	23	790.38	5.81	0.04	444.17
10.	$S_{relative.age} \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	24	792.58	8.01	0.01	740.95
11.	$S_{year} \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	29	793.86	9.29	0.01	433.64
12.	$S_{attachment} \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	27	798.23	13.66	0.00	442.73
13.	$S_{time} \cdot p_{year + time} \cdot r_{attachment} \cdot F_{0.98}$	34	805.01	20.44	0.00	432.71
5.	$S_{time} \cdot p_{time} \cdot r_{time} \cdot F_{time}$	46	987.03	202.46	0.00	575.34

Release methodology

We constrained the most parsimonious post-release survival model (model 1, Table 2) to make inferences about the effects of release management variables on survival. Julian release date ($S_{release.date}$) was the best supported model (model 6, Table 3). It had a QAICc weight of 0.79, with ΔQAICc > 4 and the evidence ratio showed it has 8.77 times better support than the next best model for age of release (model 7). Figure 3 illustrates the functional relationship between survival probability and release date (β = -0.023, SE ± 0.007): individuals released in late August (77.1 %, SE ± 2.6 %) had a higher probability of surviving than those released in late October (46.2 %, SE ± 5.5 %). Although release date and release age are correlated, release date is a better predictor of survival as it is 8.77 times better supported than model 7 that includes age at release (Table 3).

Relative age at release had little support (model 9, Table 3) as the β spanned zero (β = -0.004, SE ± 0.01) indicating relative age at release was not important in influencing survival rate.

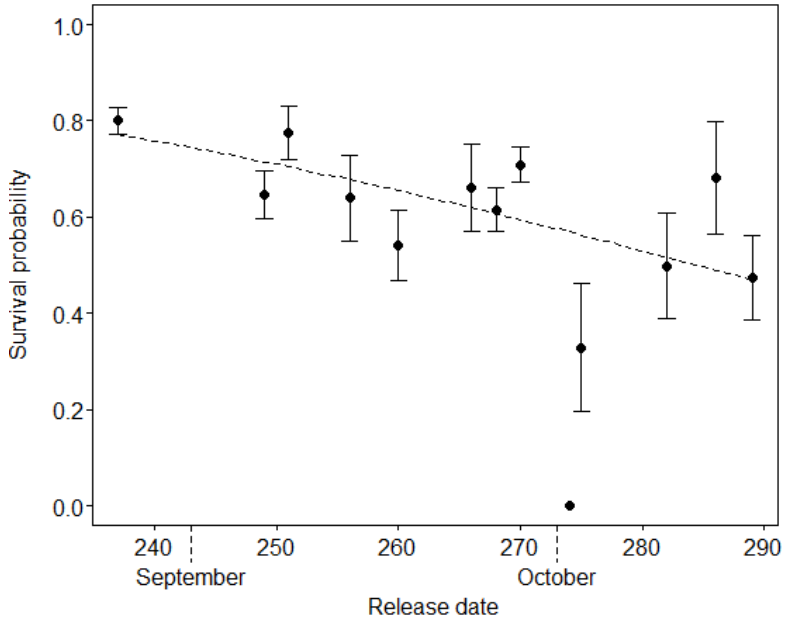

Fig. 3. Estimated monthly survival probabilities for the first six months after release for Great Bustards cohorts released at different time from August to October. Predicted model values are plotted as a line through the survival estimates (model 6).

The other release management hypothesis had no support for inferring strong effects. Release cohort size received little support (model 8, Table 3) with no clear indication of influence (β = 0.032, SE ± 0.017).

Survival rates were comparable between years (estimated from model 10, Table 3, Fig. 4). The attachment type model (model 11, Table 3, Fig. 5) received no support and there was little difference in the survival rate between transmitter types although birds without transmitters had a lower estimated survival.

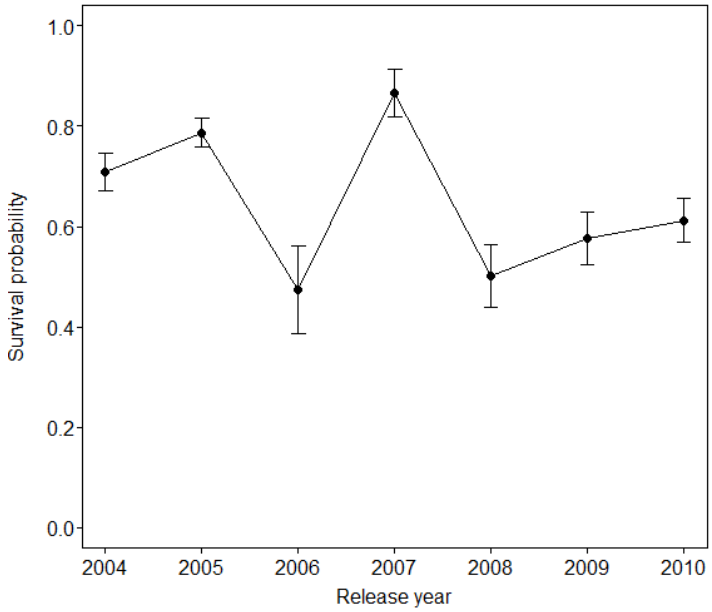

Fig. 4. Estimated monthly survival probabilities for the first six months after release for captive-reared Great Bustards released between 2004 and 2010. Values estimated from Model 10 (not shown in table) with standard errors.

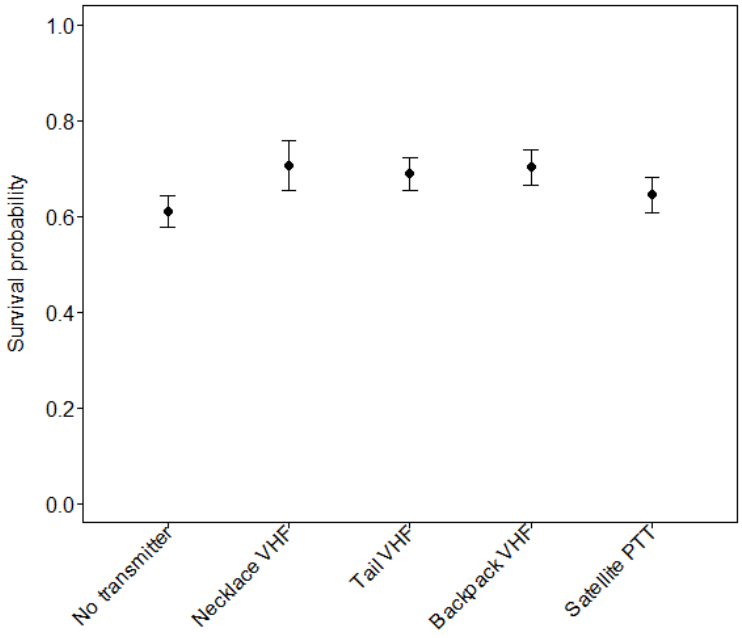

Fig. 5. Estimated monthly survival probabilities for the first six months after release for captive-reared Great Bustards with different monitoring devices. Values estimated from Model 11 with standard errors.

Discussion

Post-release survival during the critical period of vulnerability

The probability of a captive-reared Great Bustard surviving for six months following release (10 %) was lower than previously estimated first year survival, 18 % (Burnside et al. 2012). This is due to continued low survival rates for 2009 and 2010 releases. Similarly low survival rates have been found in other bustard release programs. Survival of captive-reared Houbara Bustard *Chlamydotis undulata macqueenii* two months after release was 36 % to 48 % which is comparable over the similar period to our estimates (Combreau & Smith 1998). Captive-reared Great Bustards released in Germany using similar methods also experience high mortality due mainly to predation, with variable survival rates of 15 – 40 % from release in autumn to the following spring (Eisenberg 2008). Typically, captive-reared birds have shown high rates of mortality after release, in game birds for example. Captive-reared Grey Partridge *Perdix perdix* have shown 10 % survival over the first year after release due mainly to predation (Parish & Sotherton 2007), while Northern Bobwhites *Colinus virginianus* had variable survival rates of 12 – 37 % during the first year after release (Terhune et al. 2007).

Generally survival rates increase with time after release, often being lowest in the first months after release and gradually increasing (Brown et al. 2006; Tavecchia et al. 2009; Wear et al. 2005). Here, although we observed lower survival in the first months with some evidence of increase, survival rates remained relatively low compared to the higher annual survival observed once individuals pass the six month critical period (74.6 % annually, Burnside et al. 2012).

The period of six months vulnerability to mortality in this population is long relative to rates reported in some other species. In Crested Coot *Fulica cristata* the costly post-release period lasted one month when a third of all mortality happened (Tavecchia et al. 2009). In contrast, an extended period of vulnerability of 12 months has been reported in Red-billed Curassows *Crax blumenbachii* (Bernardo et al. 2011).

The established causes of mortality suggest that captive-reared individuals are more vulnerable to predation and collisions compared with wild-born Great Bustards of the same age (Martin et al. 2007). The prolonged period of vulnerability observed here indicates an absence of appropriate behavioural traits at release (as a result of captive-rearing) and suggests that bustards only acquire the correct behaviours for avoiding collision and predation after a prolonged period in the wild.

Great Bustards are already known to be vulnerable to collision (Janss & Ferrer 2000; Martin & Shaw 2010). The captive-reared individuals have limited opportunity to fly before release due to the confined rearing and quarantine conditions. In the wild during initial learning flights, the open steppe may be more forgiving to mistakes than the UK farmland environment especially when combined with the weight of the birds and lack of flying experience. This likely leads to increased probability of collisions with fences and powerlines.

Traditionally, vulnerability to predation in captive-reared birds is attributed to absence of predator recognition (Griffin & Blumstein 2000). Firstly, the role of maternally transmitted experience is likely to be important in Great Bustards as they have extended parental care of 6 – 12 months. Although the extent to which mothers teach chicks remains unknown, it has been shown that mothers teach migration routes to their chicks (Palacin et al. 2011). High predation rates have been observed in many reintroduced bird species (Green et al. 2005; Jones & Merton 2012; Parish & Sotherton 2007; White et al. 2005). The usual response is to attempt predator training as part of the captive-rearing process, although there is little evidence to support its functionality in birds (Griffith et al. 1989; van Heezik et al. 1999).

Secondly, chronic stress could be an alternative explanation for vulnerability to predation in reintroduced animals (reviewed by Dickens et al. 2010). In short, when a stimulus or "stressor" like a predator approaching occurs, an acute physiological response is triggered which, in turn, leads to a behavioural action like the 'fight-or-flight' response. However, when animals are repeatedly stressed, the feedback mechanism becomes disrupted resulting in an attenuation of the response. This process has been empirically demonstrated in Starlings *Sturnus vulgaris* and Chukar *Alectoris chukar* held in captivity which both showed temporary loss of fight-or-flight response (Dickens et al. 2009; Dickens & Romero 2009). During the reintroduction process, Great Bustards undergo long-distance transport and it is necessary to capture individuals many times during rearing, quarantine and prior to release. Hypothetically this could lead to chronic stress or habituation to threats through repeated non-lethal stress events. Any impaired functionality or slowing of this response could be lethal for individuals that subsequently encounter threats in the wild.

Release methods to improve survival

The post-release survival probability of captive-reared Great Bustards was influenced by the date of release. The best supported model indicated that post-release survival probability of the juvenile birds was negatively correlated with release date (starting in August and ending in October). Delayed releases of other species have also shown increased mortality, although, generally these releases were delayed over longer periods of a year or more, such as for Marbled Teal *Marmaronetta angustirostris* and Hawiian Geese *Branta sandvicensis* (Black et al. 1997; Green et al. 2005).

Because age of release is positively correlated with release date and associated changes in seasonality, the interpretation of the cause of reduced survival could be confounded. We have attempted to control for this correlation by modelling relative release age, and found no relationship of relative age within release groups. However, this approach has limitations as the range of age differences within groups was less than between release dates (22 vs 52 days respectively). The relative importance of these factors could only be resolved conclusively with experimental release of young and old cohorts at different times which is impractical given the constraints of the release project. Nevertheless, in the case of captive-reared Great Bustards, the

evidence suggests that it may be beneficial for survival to release individuals in August and September rather than October.

Seasonality and age at release have both been shown to be important factors in the survival of reintroduced species (Bernardo et al. 2011). Seasonality may lead to longer nights, colder and wetter weather, different behaviour of predators or people and differences in food availability. Although most confirmed causes of mortality were predation and collision both these causes could be influenced by the condition of the birds which, in turn, could be influenced by environmental conditions related to season.

Increasing age at release which can also be seen as extending time in captivity has been shown to reduce the ability to adapt to the wild in birds and mammals (Wallace 2000). Some animals may only have a finite period during early life when they have the ability to acquire behavioural mechanisms, such as predator recognition and avoidance (Griffin & Blumstein 2000; Teixeira et al. 2007). Released Pink Pigeon *Columba mayeri* showed decreased survival when released after 150 days old (Swinnerton 2001). The ability to adapt in the wild may decrease further with age as long-lived birds can often show higher mortality rates when released as adults (Sarrazin et al. 1994). It has been suggested that there is a trend for improved survival the sooner birds are released after fledging (Jones & Merton 2012), although there are exceptions, such as with Griffon Vultures *Gyps fulvus fulvus* (Sarrazin & Legendre 2000).

Monitoring method

The type of transmitter attachment did not influence the resighting rates of individuals. This is due to the restriction of resightings to the release site and the experienced field staff present at the site. If bustards were at the release site they were often easy to locate. Therefore, the probability of resighting within the release site was high regardless of the transmitter used. In contrast, the presence of a tracking device substantially improved the probability of recovering dead individuals. Birds carrying backpack devices were much more likely to be recovered than birds without devices, providing valuable data on causes of mortality. We did not find support for the influence of group size nor transmitter attachment method on survival rates over the first six months after release.

Conclusions

We chose to investigate the six month post-release survival of captive-reared Great Bustards because it was evident that this period of vulnerability would have a critical impact on the number of individuals available to help found a new population (Burnside et al. 2012). However, the creation of a persistent and self-sustaining population will ultimately be determined by the presence of suitable habitat (Fischer & Lindenmayer 2000; Griffith et al. 1989; Wolf et al. 1998). High

mortality is a setback for the addition of founders which buffer demographic stochastic events when the population is small (Caughley 1994). The improvement of survival of released juveniles is desirable especially when there is a limited stock from which to release. Moreover, the number of founders will likely increase the probability of establishment but is not a guarantee of success or failure (Armstrong & Seddon 2008; Seddon et al. 2007).

The application of release methodologies and monitoring will vary between reintroduction projects and the species involved. Nevertheless, here we have shown that monitoring of reintroductions can help to inform management decisions including our key recommendation that juvenile Great Bustards are released soon after fledging in August or September rather than October. Our results may be of interest for other bird release programs, for example, to other threatened bustards such as the critically endangered Great Indian Bustard (Dutta et al. 2011), and for the release of other long-lived, captive-reared animals.

Acknowledgements

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Image 5. This female, called T5, flew independently to Normandy France where she spent the winter. She returned to the UK the following spring, despite showing strong habituation to humans. She carried a VHF transmitter. Photograph by John Burnside, taken in France.

Chapter 4: Post-release movements of captive-reared Great Bustards

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Manuscript

Author's contributions

RJB: statistical analysis, data collection, manuscript preparation
AD: Data collection,
KA: Manuscript improvement
IC: Manuscript improvement
DW: Project creator
TS: Manuscript and study design improvement

Abstract

This paper presents the observations of post-release movements and range size of reintroduced captive-reared Great Bustards *Otis tarda* released in the United Kingdom. Movements and range were calculated from Argos PTT, release site monitoring and general public sightings of individually marked birds. Dispersal data were not available for many individuals due to high mortality, however, 33 % of 102 birds assessed moved away from the immediate release area in the first year, 50% of these did not return due to mortality. Birds gradually left the vicinity of release site from release in September until January with long distance movements tending to be towards the south, the maximum distance in the first 12 months post-release was 920 km. Movements of seven birds that established to three years old all showed large "out and back" movements from the release site (median maximum distance 71.9 Km, range 11.3 - 90.8 Km.). All individuals incorporated the release area into their range and returned for varying periods (mean 87 days per year). Using home range estimations, birds traversed large areas (minimum convex polygon mean: 2,727.7 km^2, range 20.4 – 8,997.2 km^2). Distances from the release site tended to have bimodal distribution causing a large increase in home range estimates. Furthermore, kernel density probability of PTT data indicated the utilised areas would be smaller (70km^2). The site of first breeding attempts for the seven individuals were centred on the release site and its immediate surroundings, despite earlier dispersive movements. Large movements increase the difficultly of managing habitats to benefit Great Bustards and hinders detailed monitoring of released individuals.

Keywords: dispersal, migratory orientation, monitoring, *Otis tarda*, reintroduction, UK

Introduction

Understanding the process of population establishment is fundamental to improving outcomes of reintroductions (Armstrong & Seddon 2008; Seddon et al. 2007). Reintroduction aims to establish a self-sustaining population of an organism in an area of its historical range from where it has been lost (IUCN 1998). Reintroduction is usually achieved by releasing individuals into a target area to create a founder population. Propagule pressure and the small population paradigm predict that a larger initial population size will increase the probability of successful establishment (Caughley 1994; Lockwood et al. 2005). The evidence from systematic reviews of the factors effecting reintroduction success support these predictions and consequently many reintroductions endeavour to release as many individuals as possible (Fischer & Lindenmayer 2000; Griffith et al. 1989; Wolf et al. 1998).

There is often a disparity between the number of individuals released and the initial population size because individuals are lost through post-release dispersal and mortality (Armstrong & Seddon 2008). An elevated post-release mortality is common in reintroductions and reduces initial population size (Burnside et al. 2012; Moseby et al. 2011; Parish & Sotherton 2007). However, extensive movements or high dispersal rates can also undermine efforts to establish a population (Le Gouar et al. 2012). Dispersal, in the context of a reintroduction, is defined as any temporary or permanent movement away from the release site (Le Gouar et al. 2012). Long distance post-release dispersal, high dispersal rates and low release site fidelity are important management considerations (Clarke & Schedvin 1997; Hardman & Moro 2006; Mitchell et al. 2011; Tweed et al. 2003; van Heezik et al. 2009). Individuals leaving the release area and not returning are effectively removed from the initial population and will not form part of future breeding groups (Roe et al. 2010; Tweed et al. 2003). Consequently, high dispersal rates can slow population growth or lead to establishment failure (Mihoub et al. 2011). For example, after controlling for mortality, dispersal of griffon vultures *Gyps fulvus* from release areas was responsible for the failure of reintroduction attempts at multiple release sites (Le Gouar *et al.* 2008).

The Great Bustard *Otis tarda* is a large sexually dimorphic farmland bird with a lek mating system. It became extinct as a breeding species in the United Kingdom (UK) around the 1830s and is currently categorised as globally Vulnerable to extinction (IUCN 2012). In 2004, a trial reintroduction began on Salisbury Plain, UK, to restore a population in southwest England. The ongoing UK reintroduction releases captive-reared chicks transported from a donor population in Russia, which are obligate long-distance winter migrants (Watzke 2007).

Here, we use long-term sightings data from individually marked Great Bustards *Otis tarda* to investigate dispersal and home range size. We divided the analysis into two sections: First, we investigated post-release movements for all juvenile birds released for one year after release to establish if, and what, post-release effects occur. Second, we investigated the movements and home

range size of released Great Bustards that survived to 3 years old, the approximate age of maturity. Our aim was to quantify the variation in post-release movements and their implication for reintroduction of the species.

Methods

Reintroduction and marking

Reintroduced Great Bustards came from a donor population east of the Volga River in the Saratov Oblast, Russian Federation (50°50' N, 46°12'E). Eggs rescued from destruction during the cultivation of farmland are incubated in Russia after which chicks are raised using a dehumanisation suit to reduce the risk of human imprinting. From 2004 to 2010, 147 Great Bustard chicks, aged between 30-70 days, were transported *c*. 3,500 km to the UK where they underwent a compulsory one month quarantine period. Fifteen birds died prior to release and ten birds were deemed to be unfit for release. A total of 122 captive-reared Great Bustards were released at the same site on Salisbury Plain between 26 August and 17 October each year. Release group sizes varied each year. All individuals were fitted with coloured patagial tags allowing each individual to be identified. Additionally, 28 individuals were fitted with harness-mounted backpacks Argos/GPS enabled LC4TM platform transmitter terminals (PTT; Microwave Telemetry Inc., Columbia, USA), 105 gram for males and 40 g units for females; 18 individuals were fitted with harness-mounted backpack Biotrack TW-3 72 g VHF transmitters; 10 females were fitted with necklace-mounted Biotrack TW-3 15.5 g VHF transmitters. Finally, 25 individuals were fitted with tail-mounted Biotrack TW-3 12.2 g VHF transmitters.

Monitoring

This study covers the monitoring period of August 2005 to September 2011. We did not include juveniles released in 2004 in the analysis of first-year movements because resighting data were not available and therefore only includes cohorts from 2005-2010, reducing the juvenile sample size to 102. From all birds released, seven individuals had reached or passed age three (36 months after release) by September 2011. The seven individuals were released in 2004 (1 female), 2005 (2 females, 1 male), 2006 (1 female), 2007 (1 male), 2008 (1 female). Project staff were present on the release site on a near weekly basis thus enabling a near-continuous monitoring effort at the release site. The release site was searched by driving and searching for birds using telescopes from vantage points or located using radio-tracking. Searches were not undertaken in systematic survey fashion, but attempted to locate all birds known to be alive. Search radius at the release site was restricted due to the layout of roads and the adjacent military training areas to approximately a 2 km radius from the release pen. The ability to search beyond the release site was limited due to the time, distances and unpredictability of the movement of the small number of birds. Light aircraft with radio-tracking was used for a period to attempt to locate birds beyond the release site. Dispersal

studies can be confounded by study area effects if dispersal distances are greater than the area subjected to regular monitoring effort (Baker et al. 1995; Franzen & Nilsson 2007). However, this was not a major problem in the present study due to the Great Bustard's large size, its rarity in the UK, project publicity and the presence of easily identifiable patagial tags. There were regular reports from bird observatories, nature reserves and other areas frequented by birdwatchers and the general public frequently identified dispersal locations. Compared to its rarity and small number of individuals, the comparative reporting rate was relatively high. Overall, adults aged 1 - 3 years old were re-sighted at least once a month for nine months of the year.

All sightings with an error of 1km or less (from the grid reference reported) were mapped in ArcView GIS in WGS 84 UTM 30N projection. Re-sightings that did not allow individual identification were removed. Satellite telemetry data were collected from the Argos Data Collection and Location System, where they are rated according to location accuracy. Here, we use only locations which are calculated from more than 4 transmissions (location classes 0 - 3), excluding those using 3 or less transmissions (location classes A and B), to ensure that location data is accurate to approximately 150m - 1000m.

Dispersal measurements

All released individuals were included in the juvenile analysis to examine post-release effects for one year after release, while to examine dispersal and release site fidelity in established individuals we used seven individuals that survived to three years. All movements are described in relation to the release site. For juveniles, we defined two metrics of movement, a) Maximum monthly distance which was the farthest record per month from the release site for each individual each month; and b) its corresponding direction in degrees. For the seven established individuals that survived 36 months after release we defined four metrics of movement; c) Maximum monthly distance; and d) its corresponding direction in degrees; e) Release site fidelity which was the number of days that individual was resighted within the release site monitoring area each year (2 km radius of release pen); and f) Home range size was used to estimate the areas traversed and potential size of area needed for an individuals. Range was estimated using all records for each individual.

There are various methods for calculating home range size and all can give different results from the same dataset (Boulanger & White 1990). Here we use minimum convex polygon (MCP) 100% including all records; MCP 95 % excluding 5 % of the extreme points (Mohr 1947); and lastly utilization distribution kernel density probability (UDKD) with 95 % probability of occurrence (Worton 1989). MCP is often criticised because it overestimates the area utilised by an individual whereas kernel density will give a better prediction of area utilised but it will miss corridors between these areas (Kie et al. 2010). Since kernal density utilises probabilities based on occurrences, sampling bias towards one area will lead to over-estimated probabilities in that area (Frair et al. 2004). Non-PTT individuals will be subject to this bias as more records will be present

at the release site than away. Therefore, using MCP for these data will not violate assumptions, but will give an estimate of the areas they traversed. Conversely, the data from the PTT are suitable for kernel density estimation and can give insight into how much MCP may overestimate utilised area. We used three methods for the Argos PTT data individual because the data provides high resolution on the intermediate areas utilised. Whilst we used MCP for individuals that only had resighting histories. For the adult male who carried Argos PTTs which fixed once per day at midnight, we also calculated the mean daily movement. Home ranges were calculated with adehabitatHR package in R Gui (Calenge 2006).

Lastly, we report 'natal' dispersal distance using the release site as a surrogate for the natal site. We identified the distances to the first nesting attempts and first male display behaviours.

Statistics analysis

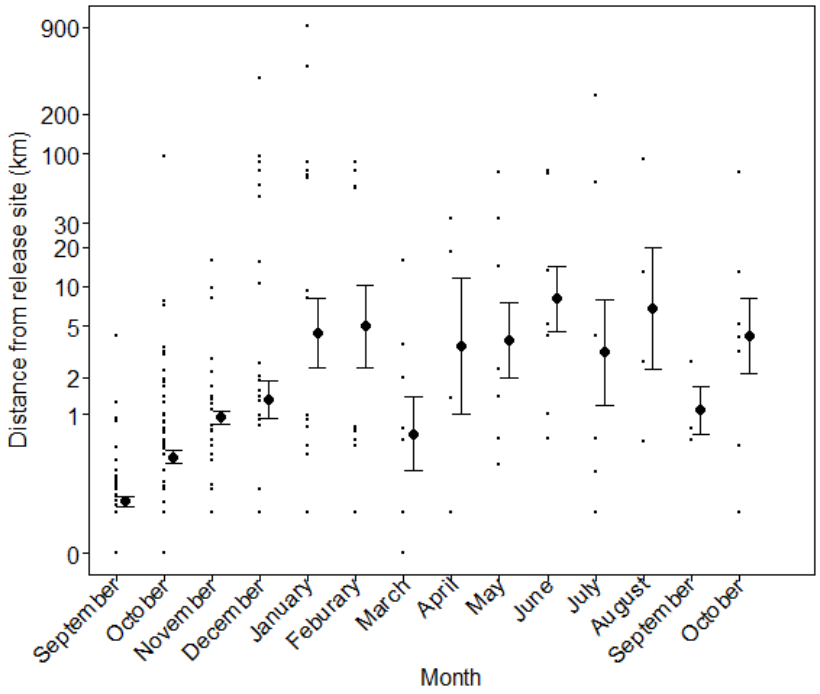
Hypothesis testing about distances and fidelity was carried out using generalized linear mixed models with individual bird ID & release year set as random effects to control for pseudo-replication of repeated measures. Individual variables were included in a model and tested by ANOVA against the null model with no variable (intercept only) for a significant reduction in deviance (Crawley 2007). Dispersal distances were log-transformed and analysed with Gaussian errors. To test for randomness in direction of movements from the release site, we categorised records according to the four quadrants of the compass: northeast, southeast, southwest and northwest. The counts of records in each quadrant were tested against a random distribution using chi-square test. R Gui statistical programme was used for all analysis (R Core Team, 2012).

Results

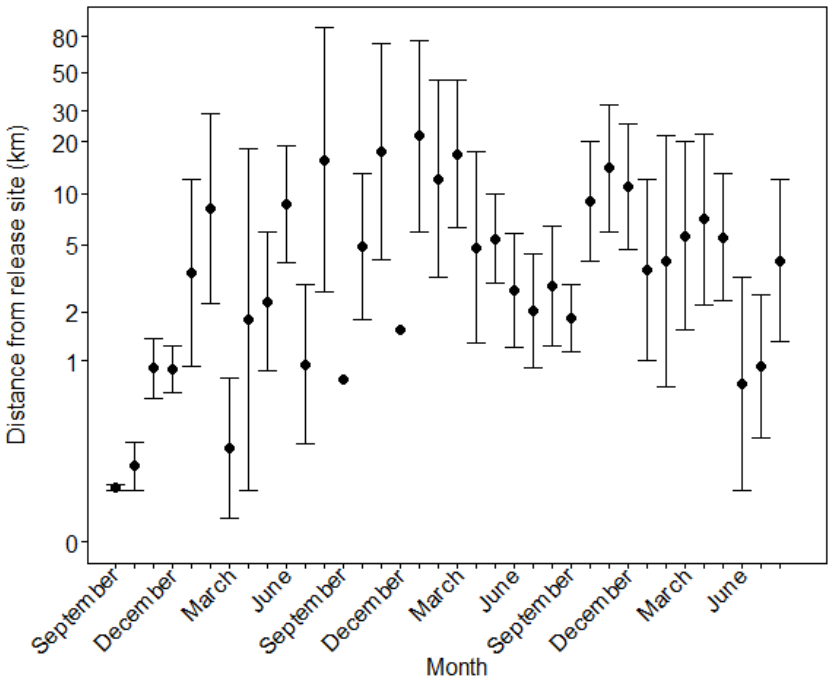
Post-release effects on juvenile movements

A total of 330 maximum monthly locations were recorded for the 102 juvenile Great Bustards in the first year after release. Due to high mortality, the sample size of individuals drops over the 12 month period. Thirty four juveniles (33 %) were recorded to move greater than 2 km from the release site. Seventeen (50 %) of these juveniles were permanently lost from the population during movement away from the release site: five individuals made long distance movements > 250 km from the release site; eight individuals were confirmed dead and four were not recorded again.

Individuals showed high variability in distances moved from the release site (Fig. 1a). There was a gradual increase in the maximum distances moved from the release site from September to January after which monthly maximum distance stabilised (Fig. 1a). There was no difference in the distances moved between the sexes (GLMM, $\chi^2 = 0.70$, d.f. = 1, $p = 0.40$). Five individuals made substantial long-distance movements of greater than 250 km. The maximum recorded distance from the release site was 920.2 km.

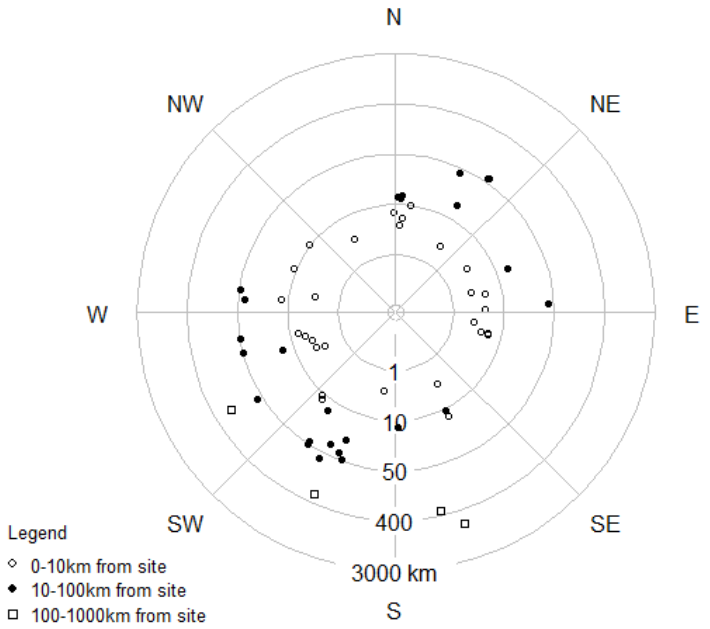


a)

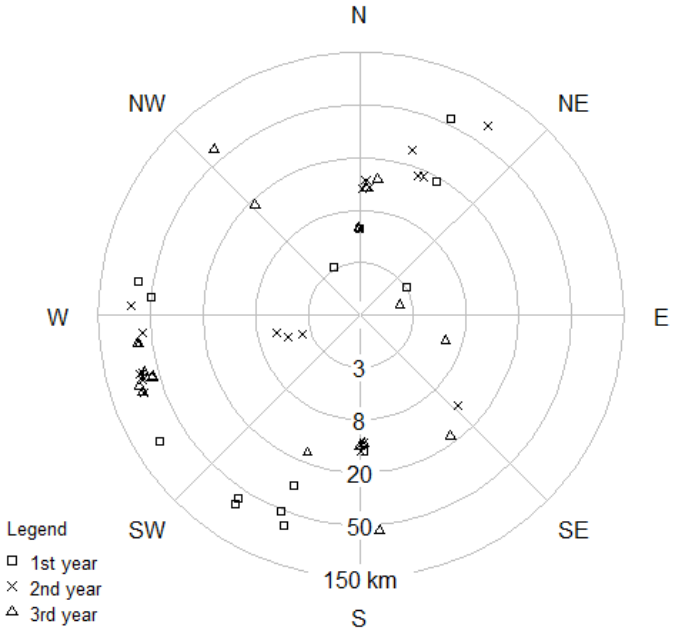


b)

Figure 1. (a) Mean maximum distances (log scale) and standard error (vertical solid lines) of movements by 102 captive-reared juvenile Great Bustards for one year after release in the UK (2005-2010). Smaller adjacent black dots are individual records. (b) Mean maximum distances moved by seven adult captive-reared Great Bustards for 36 months after release (first record). The dot is the mean with standard error bars (vertical solid lines).



a)



b)

Figure 2. Plot showing the directional movements of (a) juvenile captive-reared Great Bustards for the first year after release in the UK. Distance scale is logarithmic (km) and each symbol is one record of an individual. Data is split into three categories of distances from the release site (centre) for clarity (330 records for 102 individuals). (b) Direction of movements from release site for seven established Great Bustards which reached 3 years old categorised by year after release.

The direction of juvenile movements close to the release site were randomly distributed (2 – 10 km, $\chi^2 = 0.9$, d.f. = 3, p = 0.82, Fig. 2a), while movements farther were non-randomly distributed southwest and northeast (10 – 100 km: $\chi^2 = 23.3$, df = 3, $p < 0.001$, Fig. 2a). Movements > 100km were all in southern directions but could not be statistically tested due to small sample size of five (Fig. 2a).

Post-release movements of established individuals

For the seven individuals (two males and five females) that reached three years after release, a total of 877 unique sightings were recorded for non-PTT individuals (mean 175 ± 44SE per individual), resulting in a total of 125 maximum monthly sightings (mean 20.8 ± 3SE per individual). For the male with an Argos PTT, there were 952 unique fixes and 36 maximum monthly records. The mean daily movement from Argos PTT male was 0.51 km (s.d. 3.5 km; range 0 km – 28.79 km).

Established individuals showed a similar pattern after release as all released birds, gradually moving away from the release site in the first four months and then stabilising (Fig. 1b). All individuals moved far from the release site and the median maximum distance moved was 71.9 km (range 11.3 - 90.8 km). The median maximum distance for each year was: 1st year, 44.5 km (range 1.4 - 90.8km); 2nd year 26.4 (range 5.1 - 80.4 km); and 3rd year 62.3 km (range 1.7 - 83.4 km). Six of the seven individuals had bimodal distributions while one female had a uni-modal distribution (Fig. 3).

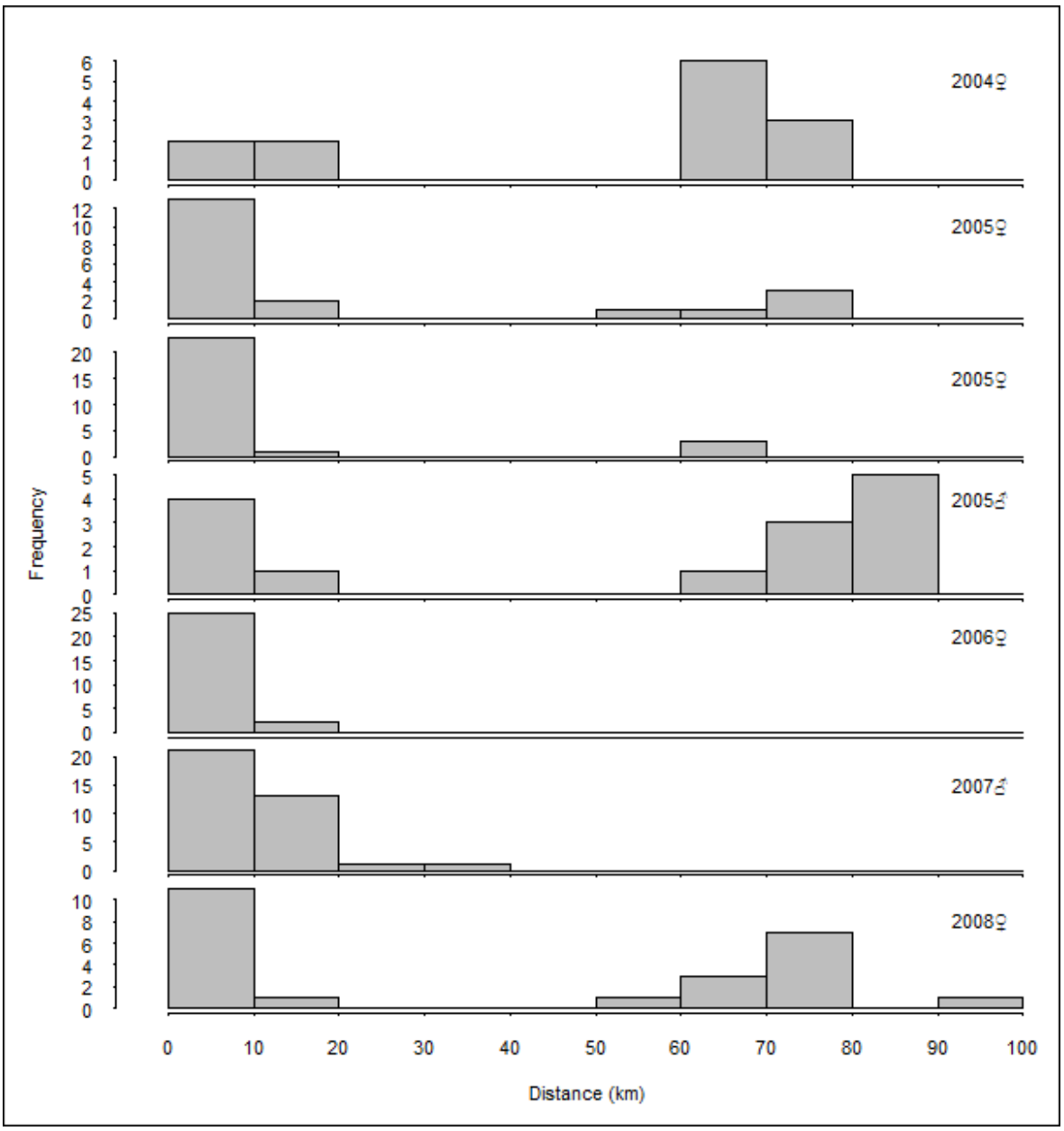
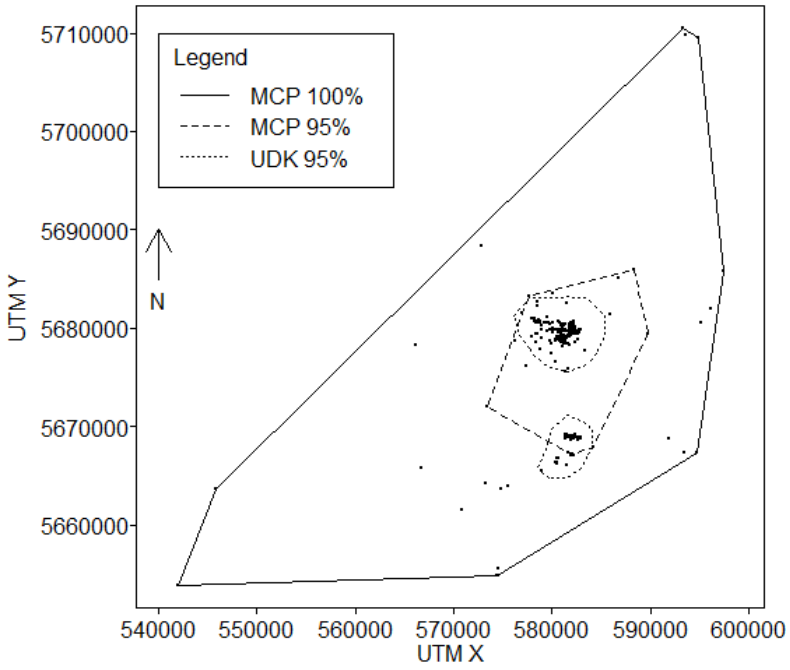
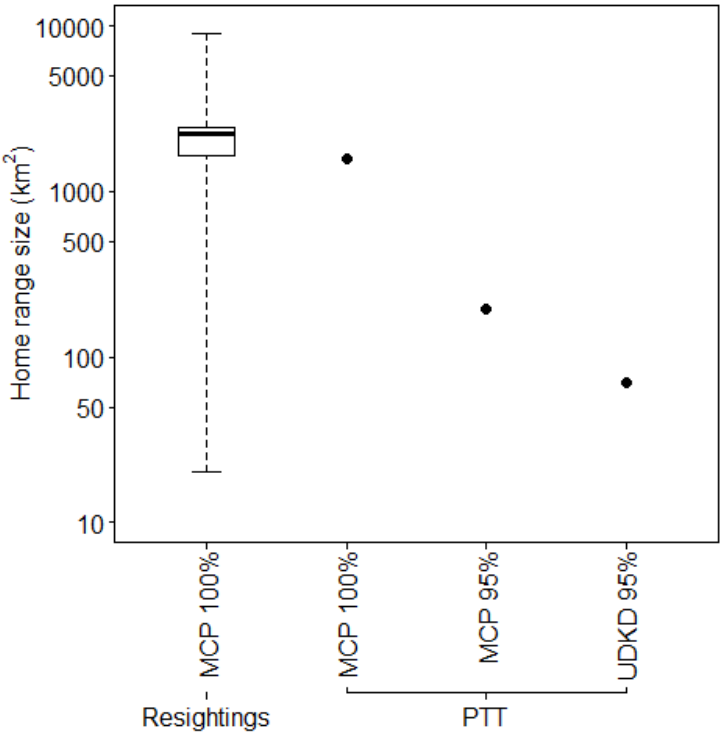


Fig. 3. Histograms showing the frequencies of the maximum monthly distances (Km) travelled by seven Great Bustards from the release site in the UK (two males & five females) released between 2004 and 2008..



a)



b)

Figure 4. (a) Home range size estimates for great bustard named P5 from three years of daily Argos PTT locations (952 PTT fixes, black dots). (b) shows the home range size (log scale) estimates for birds with only resightings and male PTT bird (P5 •). Legend explanation: MPC 100% = minimum convex polygon, including 100% of records, MCP 95 % = minimum convex polygon, including 95% of records, UDK 95% = utilization distribution kernel density probability, with 95% probability of a record occurring. Universal Transverse Mercator (UTM) is used and is measured in metres.

There were no significant difference in the distance moved each year between the sexes (GLMM, $\chi^2 = 0.08$, df = 1, $p = 0.77$). The maximum distance travelled in the 2nd and 3rd years were significantly positively correlated with the maximum juvenile movement (GLMM, $\chi^2 = 6.6$, d.f. = 1, $p < 0.001$). The direction of movements beyond the release area were random in the first year ($\chi^2 = 5$, df = 3, $p = 0.17$, Fig. 2b), and 2nd year ($\chi^2 = 2.4$, d.f. = 3, $p = 0.49$, Fig. 2b), whilst 3rd year movements were significantly in the southwest ($\chi^2 = 14.2$, df = 3, $p < 0.01$, Fig. 2b).

All established birds incorporated the release site into their range and made return visits at varying frequencies each year after release (mean 87 ± 3SE days per year at release site, range = 0 – 294 days). There was no evidence of difference between years (GLMM, $\chi^2 = 1.76$, d.f. = 2, $p = 0.41$) or between the sexes (GLMM, $\chi^2 = 1.88$, d.f. = 1, $p = 0.17$).

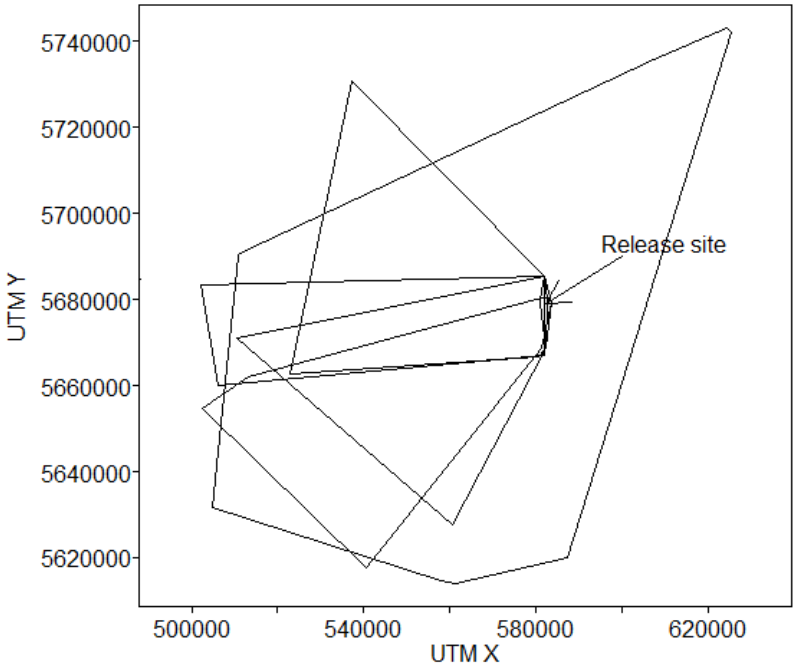


Fig. 5. Home range size estimates for Great Bustards (six individuals) using minimum convex polygon 100% during 36 months after release in the UK.

Validation of home range size technique with PTT data showed that MCP is likely to overestimate the area used but does incorporate likely corridors of movement (Fig. 4a). The mean home range size for the PTT male was estimated for MCP 100%: 1567.0 km^2, MCP 95%: 196.1 km^2, and UDK 95%: 70.0 km^2 (Fig. 4a and Fig. 5). For all individuals during the 36 month period after release, the average size of area covered estimated from MCP 100% was 2,727.7 km^2 ± 1,088.9 SE (range 20.4 – 8,997.2 km^2, Fig. 4b). MCP 100% showed comparable estimates of home range size between PTT birds and resighted birds. Using MCP 100%, range size was greatest in the first year after release (Year 1: 1354.2 km^2 ± 1224.1), and dropped in the 2nd and 3rd year (Year 2: 499.6 km^2 ±

295.6 SE; Year 3: 771.4 km^2 ± 299.7 SE) although the differences were not significant (ANOVA, $F = 0.39$ on d.f. = 2 and 17, $p = 0.6805$).

Natal site fidelity

By 2010, the two males and five females from release years 2004-2008 bred or showed courtship behaviour. All seven birds were observed at the release site during the breeding season in years 2007 – 2011. The two males showed displaying behaviour and four females nested within 2 km of the release site, with a fifth female showing nesting behaviour 10 km away.

Discussion

Reintroduction projects are usually more likely to succeed if a high proportion of released individuals remain in the release area or at least incorporate the release area into their home range (Mitchell et al. 2011). This increases the chances of creating a unified population and breeding group. Additionally, it allows control of the early environment and reduces the investment needed to monitor released individuals (Hardman & Moro 2006; Le Gouar et al. 2012). We identified four important patterns of movement of reintroduced captive-reared Great Bustards: 1) juveniles released in the summer and autumn are likely to move away from the release site in the months after release 2) juveniles can easily move up to 100km from the release area with longer movements in southerly directions, 3) established individuals showed similar patterns of long movements but also returned to the release site regularly during 'out-and-back' movements giving large ranges to the individuals; and 4) the release site was adopted as the "natal lek" with mature adults returning to breed.

Post-release effects on juvenile movements

The assessment of post-release effects on dispersal is confounded by the high mortality experienced by the released individuals. As a result, many individuals may die before getting the chance to disperse, or conversely, not return to the release area after dispersal due to death. Great Bustards began gradually moving farther from the release site from release until January. Within 10 km of the release site these movements were in random directions, whereas distances greater than 10 km were predominantly south-west like the direction of known migration routes in the donor population (Watzke 2007). However, distances covered were not similar to the donor population's 1000 km migration, apart from the individual that moved 920 km. This suggests that directional preference may be hard-wired but migratory distances are learnt. Directional preference by naïve first year juveniles has been observed in other experimentally displaced naïve migrants, for example, White Storks *Ciconia ciconia*, Blue-winged Teal *Anas discors* and Herring Gulls *Larus argentatus* showed strong direction preferences based on the population from which they were taken but require the presence of conspecifics to learn the exact migration route and stop-off points

(Chernetsov et al. 2004; Itonaga et al. 2011; Newton 2008). Therefore it is likely that for complete learning of the migratory pathways, Great Bustards require experienced conspecifics.

Movements of established individuals

All seven of the Great Bustards that established and survived to three years showed movements away from the monitored release site during the juvenile period and their second and third year. Great Bustards would return to the release site intermittently. The movement patterns are consistent with dispersive migration seen in other Great Bustard populations with birds moving outward from the natal site and returning, often seasonally (Alonso et al. 1995; Alonso et al. 1998; Alonso et al. 2000). There was some evidence of seasonal movement in the released individuals. Dispersive migration differs from traditional migration as it can occur within the breeding range, it may not be driven by loss of food and it tends to involve shorter distances (Newton 2008). These 'out-and-back' movements between areas have been seen in a wide range of resident species including Grey Heron *Ardea cinerea*, Common Buzzard *Buteo buteo*, Mute Swan *Cygnus olor* and Spruce Grouse *Dendragapus Canadensis* (Herzog & Keppie 1980; Wernham et al. 2002).

Adults and breeding birds showed fidelity to the release site by including it in their range. The mechanism by which the release site becomes imprinted is still unknown but potentially is either through the presence of conspecifics immediately after release or, in this case, the absence of other leks to visit (Alonso et al. 2004; Martin et al. 2008). Since there is currently only one 'natal' site in the UK, it is reasonable for individuals to return here to seek breeding opportunities. Alternatively, the period of time spent on site during quarantine and the fact that birds see conspecifics at the site could help anchor the birds (Mitchell et al. 2011).

Range size estimates showed that Great Bustards traverse large areas during their first three years. However, their area utilisation is much likely smaller as birds mainly moved between two or three sites. Kernal density estimation confirmed that the male with an Argos PTT spent most of his time between two areas with area utilised of 70 km^2. Therefore, as predicted the MCP method overestimates the area utilised but gives important information about the capability of Great Bustards to traverse large distances. Similar small utilised range sizes but seasonal movements have been found for other Great Bustard populations (Alonso & Alonso 1992). Furthermore, Houbara Bustard *Chlamydotis undulate u.* have shown similar multimodal distribution of distances from release sites, also leading to large ranges but actually small utilisation areas (Hingrat et al. 2004). The area needed to sustain a Great Bustard may be small, but the movements between the areas will be big. This leads to management difficulties of selecting and directing Great Bustards to pre-chosen areas or the manage habitat for them.

Conclusions and conservation implications

High post-release mortality of captive-reared Great Bustards in the UK has limited the establishment of a founder population (Burnside *et al.* 2012). The influence of dispersal will have contrasting effects. Firstly, there is a high level of movement from the release site. This will result in birds moving into unmanaged habitats and increases the resources needed to monitor birds effectively (van Heezik et al. 2009). Dispersal also tends to be a risky behaviour as animals will encounter unknown threats and potentially enter areas where habitats are unsuitable (Le Gouar et al. 2012). On the other hand, birds surviving to adulthood clearly found suitable habitat and all included the release area within their range. This has important implications for the conservation of the species because the establishment of new leks is rare in wild Great Bustard populations (Alonso *et al.* 2004).

The establishment of other leks through multiple release sites is likely to be an important factor for the successful re-establishment of a viable population (Armstrong & Wittmer 2010). Extant populations show meta-population dynamics and small isolated groups of Great Bustards have a higher probability of extinction (Alonso et al. 2004; Martin et al. 2008). Future release sites should be within 10 - 30 km from existing ones because distances greater than are less likely to be located by dispersing individuals (Martin *et al.* 2008).

These results may be useful for other bustard conservation projects trying to supplement or re-establish populations, as 12 of the 26 bustard species are categorised as Near-Threatened to Critically Endangered (IUCN, 2012). Many bustards have similar breeding systems and are facing similar threats (Dutta et al. 2011; Eisenberg 2008; Fodor et al. 1981; Gray et al. 2007; Janss & Ferrer 2000; Raihani et al. 2006; Shaw et al. 2010).

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Image 6. Four Great Bustards released in the UK from three different years foraging together in a mixed sex flock. Photograph by John Burnside.

Chapter 5: Human disturbance and conspecifics influence display site selection by Great Bustards *Otis tarda*

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Author's contributions

RJB: statistical analysis, manuscript preparation
ZV: Data collection, manuscript improvement
RJ: Manuscript improvement
SK: Data collection
GK: Data collection
TS: Manuscript improvement

Summary

Understanding habitat selection and assessing habitat quality have an important role in habitat management and prioritisation of areas for protection. However, interpretations of habitat selection and habitat quality can be confounded by social effects such as conspecific attraction. Using 7 years' data from a well monitored Great Bustard *Otis tarda* population in central Europe, we investigated the roles of human disturbance and social cues in display site selection of male Great Bustards *Otis tarda*. The spatial distribution of displaying males was best predicted by human disturbance. In addition, the number of males attending display sites was strongly correlated to the number of females present and not with disturbance. This suggests that abundance could be a misleading metric for habitat quality in social species. Our results highlight the roles of disturbance and social cues in male habitat choice, and suggest that social factors need to be taken into consideration for management of endangered populations.

Keywords*:*
conspecific attraction, habitat selection, disturbance, Great Bustard, *Otis tarda*, Hortobágy

Introduction

Understanding habitat selection and assessing habitat quality have underpinned *in situ* species conservation planning (Jones 2001, Morris 2003). It allows conservation managers to make decisions about how to manage habitats and prioritise areas for protection (Root-Bernstein and Ladle 2010). It is based on the assumptions that site selection is non-random, and that individuals assess information from multiple cues to make an optimal decision about which habitat to occupy (Jones 2001, Morris 2003, Johnson 2007). An animal's habitat choice can have important fitness consequences. In particular, breeding site choice and quality influence an individual's reproductive success (Doligez *et al.* 2002). Therefore, understanding the factors that influence habitat selection and habitat quality are important for managing habitats for endangered species. Investigating habitat selection has primarily been based on the correlation of biotic and abiotic variables with occupancy while habitat quality has been correlated with the number of individuals attending a site (Vanhorne 1983, Morris 2003).

Conspecific attraction can confound traditional interpretations of habitat selection as they violate the assumption that each individual independently assesses a site (Vanhorne 1983, Skagen and Adams 2011). Rather than sampling a location by trial and error, an individual may use the presence of conspecifics as an indicator of habitat quality, thereby reducing searching costs (Muller *et al.* 1997). In some species, the attraction to choose a site with conspecifics present may be cumulative and could lead to additive aggregation. Social attraction in habitat choice may explain why some species are more sensitive to habitat fragmentation and slow to recolonise empty habitats (Fletcher 2007). Therefore, understanding the roles of social behaviour in habitat selection can give important insights into improving the conservation biology of social species (Ahlering *et al.* 2010).

The Great Bustard *Otis tarda* is a globally threatened species (IUCN category Vulnerable). During the 19th and 20th centuries, the European populations of the species had rapidly declined. Multiple national and local extinctions have left current populations small and highly fragmented (Palacin and Alonso 2008). The Great Bustard has suffered habitat loss due to increasing non-lethal human disturbance (Lane *et al.* 2001, Suarez-Seoane *et al.* 2002, Sastre *et al.* 2009, Burnside *et al*. 2012). The negative impacts of human disturbance on many threatened species is being increasingly recognised (Gill *et al.* 2001, Frid and Dill 2002).

Effective conservation of this species requires not only an understanding of its habitat requirements, but also how social attraction influences habitat selection. Great Bustards have a breeding system which can be described on a continuum between classical lek and exploded lek as it does not fit either definition exactly (Morales *et al*. 2001). However, males gather in loose congregations and display to females. Males are not territorial and display at different sites within larger areas where display sites are concentrated. These areas contain resources for both males and females with females nesting in and around the lekking areas (Morales and Martin 2003). Habitat

modelling and direct observations have found that many areas that are deemed suitable for breeding remain unoccupied and that new leks are rarely established (Osborne *et al.* 2001, Suarez-Seoane *et al.* 2002, Alonso *et al.* 2004). Conspecific attraction has been suggested as the mechanism for the presence of unutilized habitat, and this has been corroborated by dispersal studies (Martin *et al.* 2008).

Here we use generalized linear models to investigate display site selection and attendance of Great Bustard from a small and well monitored population in Hungary. Our aims were to establish the roles of social influences and human disturbance on male display site choice. To achieve these aims we tested two hypotheses**,** 1) display site selection: are display site locations different from random areas within the greater national park in relation to human disturbance and vegetation structure, and 2) display site attendance: do females influence the number of males at display sites.

Methods

Study Area

Hortobágy National Park (henceforth HNP– Figure 1) is a large unbroken alkaline grassland in Europe, consisting of steppe interspersed with alkaline marshes (Ecsedi 2004). It is located in east Hungary (47^{o}30'N 21^{o}0' E, Figure 1), and has a Great Bustard population estimated at 140 individuals (Ecsedi 2004). It is managed through grazing of various livestock, including domestic cattle *Bos taurus* and sheep *Ovis aries*.

Survey methodology

Male Great Bustards perform conspicuous mating displays each spring. The displays are usually performed by congregations of males competing at a display site. Surveys were carried out to locate displaying males in HNP. At each observation, the number of males and females present and the centre of the group location was recorded. Any observation with ≥ 3 males present was defined as a display site. Surveys were carried out between 2000 and 2007 during the breeding seasons (March to May). Data from 2004 were excluded due to poor quality satellite images (see below), but were available for model validation after the habitat selection analysis.

Surveys covered the whole national park, and all areas were visited approximately every four days in a standardized manner. Searches occurred during peak display times in the morning (06h00 – 09h00, CET) and evening (16h00 – 19h00, CET). During each survey approximately 100 kilometres was covered using four-wheel drive vehicles, bicycles or walking. Surveys involved stopping at observation points and searching with binoculars and telescopes. The male population is estimated to be between 50 – 70 individuals, all of which can be located during the lekking season. Surveys were made by three observers with several years of fieldwork experience; they are permanently employed to monitor and manage the HNP Great Bustard population (ZV, SK and

GK). All observations were plotted in the UTM 34N reference system using the WGS1984 datum. Random habitat data were generated from random points within the boundary of the sampling area of HNP (Figure 1). We used an equal number of random points as display site points, and constrained the random points by excluding water bodies such as streams, ponds and marshes.

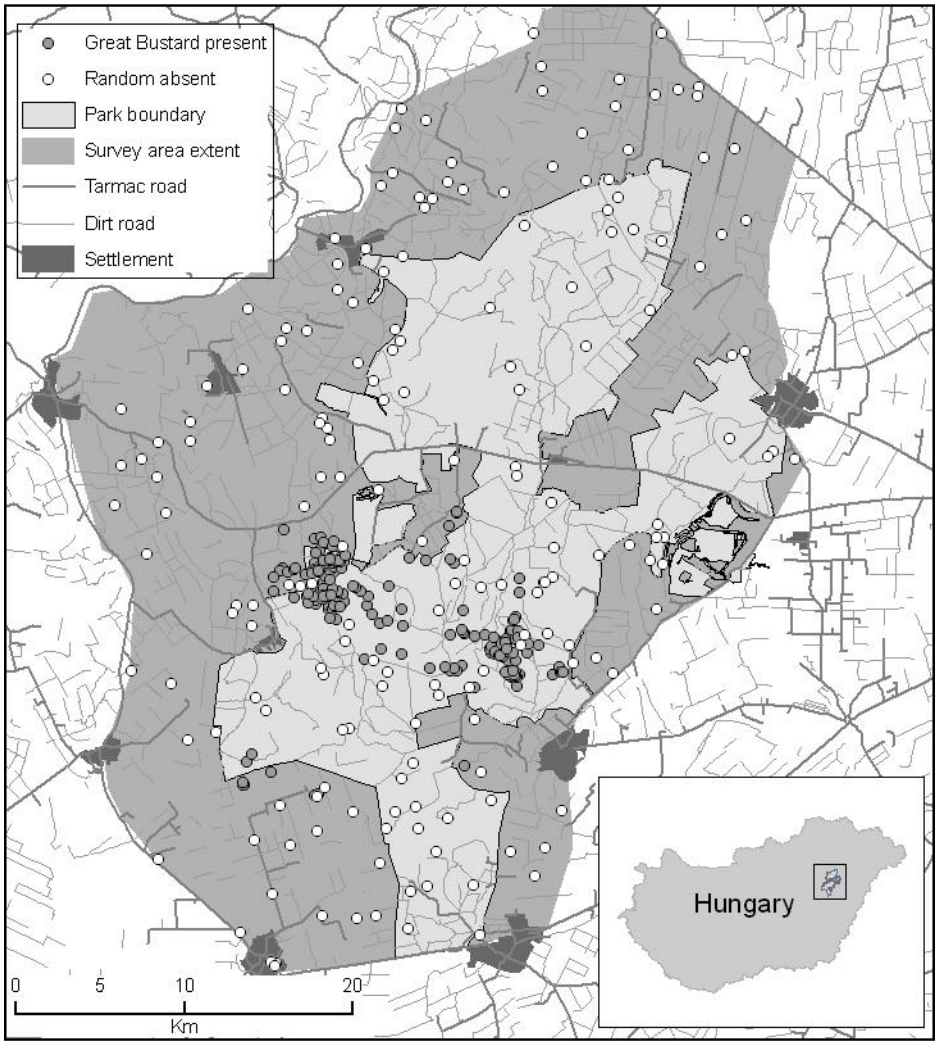

Figure 1. Location of Great Bustard display sites in Hortobágy National Park, Hungary and in the surrounding area. Surveys were carried out both within the National Park, and the grey shaded area outside.

Disturbance and habitat variables

HNP is mainly managed through traditional grazing practices that produce different intensity of grazed grassland. In addition, it is open to visitors with several dirt tracks and single lane tarmac roads for travel (Figure 1): there is only one 2-lane tarmac road dissecting the national park. These roads are potential sources of disturbance. Therefore our *a priori* hypothesis was that disturbance

by humans, and vegetation characteristics influence the spatial distribution of display sites. We identified 8 disturbance and remotely sensed variables (Table 1) based on this information. All variables, except dirt road density, were quantified at a 30m resolution whereas the latter was quantified at 1 km resolution. These scales were considered fine enough to capture variation in the variables that would be meaningful for Great Bustards. Differences between presences and random means could not be preliminarily tested due of spatial autocorrelation in the presence data. Data for tarmac and dirt roads was obtained from existing shapefiles from HNP.

Table 1. Variables representing human disturbance and vegetation structure were obtained via remote sensing (mean values ± standard error for presence sites, n = 160, and randomly chosen sites, n = 160. The difference between means was not statistically tested due to spatial autocorrelation in display sites. (Historgrams in supplementary appendix Fig. 1).

Habitat variable	Description	Display sites	Random
Dirtroad density (m/km^2)	The total distance in metres covered by dirt roads within a 1km square was used as a metric for road density	723.2 ± 55.8	821.8 ± 53.2
Distance to road (m)	Distance from observation, in metres, to nearest tarmac road. Calculated at a 30m resolution	3001.5 ± 66.4	2075.3 ± 118.2
Distance to settlement (m)	Distance from observation, in metres, to nearest settlement, human population. Calculated at a 30m resolution	5223.2 ± 112.7	5781.2 ± 229.2
Distance to sheep (m)	Distance from observation, in metres, to nearest area grazed by sheep. Calculated at a 30m resolution	1529.4 ± 77.6	2491.3 ± 152.5
Distance to cattle (m)	Distance from observation, in metres, to nearest area grazed by cattle. Calculated at a 30m resolution	1428.0 ± 64.8	2642.4 ± 160.2
TasCap brightness	Tasseled cap brightness (soil reflectance). 30m resolution	116.8 ± 1.5	114.8 ± 1.5
TasCap wetness	Tasseled cap wetness value (soil moisture). 30m resolution	-48.9 ± 1.7	-46.3 ± 1.7
TasCap greenness	Tasseled cap greenness value (chlorophyll content). 30m resolution	0.05 ± 0.01	0.05 ± 0.01

To estimate the impact of human disturbance, every farm within the study area was mapped and the number of livestock kept each year taken from the HNP's livestock register. Herdsmen keep their livestock at their farms in winter, and in spring the herds are moved to outdoors where they spend the summer. This involves moving the animals to new grazing areas outside the farm each day. HNP management estimates that an area of 1 hectare is needed to graze either 1 cattle or 10 sheep during spring (Z. Végvári, *in litt.* 2010). The total area required for livestock was calculated for each farm. A circular buffer of equivalent size was drawn around the farm which represented the area of disturbance from livestock. Observations within the grazed area were classified as 0 meters from the disturbed area. All Euclidean distances were calculated using ArcView v 9.1 and dirt road density was calculated using Hawth's Tools (Beyer 2004).

To test the influence of vegetation, we chose to use remotely sensed variables. The tasseled cap transformation provides three orthogonal vegetation indexes that are calculated from 6 bands of Landsat 7 enhanced thematic mapper plus (ETM+) data (Kauth and Thomas 1976, Crist and Cicone 1984), using coefficients for the Landsat ETM+ sensor to reduce reflectance and extract biological data (Huang *et al*. 1998). We produced three raster images for each year; tasseled cap moisture describes the surface water present, tasseled cap brightness describes the soil characteristics (i.e. bare earth present) and tasseled cap greenness describes the amount of green vegetation present. We chose Landsat 7 ETM+ multispectral satellite data because of its fine scale high resolution images (30m) and images were readily available for the study area. We used 11 scenes acquired from March, April or May from 2000-2007 (tile IDs are listed in Table S1 in online Supplementary Material). Images which had the best coverage and least cloud cover were selected. Landsat 7 images acquired after 2004 are vulnerable to Scan Line Corrector failure-OFF gaps, leaving data gaps in the image. Therefore scenes from 2004-2007 required multiple images, that were temporally close and free of cloud cover, to fill data gaps. Sufficient data was not available for 2004 to create a satisfactory mosaic and was consequently excluded from the analysis. Satellite images were downloaded from United States Geographical Service (http://www.usgs.gov). Atmospheric correction was carried out on bands 1, 2, 3, 4, 5 and 7 and images were then clipped to the extent of the study area (Figure 1), covering a total area of 3696 km^2. All image processing was done in Idrisi Kilimanjaro (Eastman 2003).

Statistical analysis

We used generalized linear models (GLMs), and model simplification to identify variables that influence bustard distribution. A maximal model was fitted with all explanatory variables and simplified by stepwise deletion of non-significant terms. Each deletion was tested for a significant increase in deviance by ANOVA. This was repeated until the minimum adequate model (MAM) contained only significant terms (Crawley 2007). Finally, ANOVA was used to test if there was a significant increase in deviance between the maximal model and the MAM. Although there is some

debate between the use of stepwise simplification and information theory for best model selection, both have received criticism for their misuse (Bolker *et al*. 2008, Burnham and Anderson 2002, Mundry 2011). Here we chose to use stepwise deletion rather than an information theoretic approach because it retains variables only if they significantly explain variation in the response variable. The objective of our parsimonious approach was to use the variables that contribute significantly in habitat selection and use these to further model site attendance. We modelled the probability of Great Bustard presence against random points within the study buffer area (Figure 1) using binary logistic regression with binomial errors.

Count and distance explanatory variables were normalized and rescaled by square-root and $\log_e(x + 1)$ transformations to improve the fit of models to the data, respectively (Crawley 2007). All pairs of explanatory variables were screened for colinearity. There were no strong correlations ($r > 0.5$) between any of the explanatory variables allowing inclusion of all explanatory variables in the multiple regressions (Freckleton 2002). To control for spatial autocorrelation in the response variables, often found in spatially aggregated lekking species (Gray *et al.* 2007), we added a spatially-weighted autologistic term described in Augustin *et al.* (1996) to all models. The term is a distance weighted sum of the number of observation points in squares surrounding the focal observation point and is calculated as follows:

$$\text{autologistic term} = \sum_{j=1}^{ki} \frac{y_j}{h_{ji}}$$

where i is the survey point, h_{ij} is the Euclidean distance between the surveyed point and the centre of the square j, k is the lag distance from i and yj is the presence or absence of a survey point within the lag distance k.

The optimal lag distance k was estimated by calculating the autologistic term for 0 m to 2000m in steps of 250m. Each estimate was then added to the maximum model and the k value that produced the greatest reduction in deviance was chosen for model simplification (Gray *et al.* 2007). The greatest reduction was found for k = 1000m. We used Moran's I to test for spatial autocorrelation within the residuals of the MAMs (Osborne *et al.* 2001).

To assess the fit of the model to the data and to validate its predictive power, we calculated area under the curve (AUC) for two separate Receiver Operating Characteristic plots (ROC). This compares the number of correctly predicted versus falsely predicted points from a set of independent data. An AUC value of 50 % indicates that the model is predicting no better than random while 100 % means it's predicted all the points correctly (Osborne et al. 2001). We used the previously excluded 2004 data points to validate the predictive power of the model for independent data. All statistics were carried out in Program R *v. 2.12.1* (R Development Core Team 2011).

Site attendance model

To investigate the influences of habitat quality and conspecifics on the number of male Great Bustards at a display site, we used counts that are all presence points. After finding the MAM for the habitat selection model, we used the remaining significant variables to construct a model which also included the number of females observed at the observation. We further examined the influence of Julian date on male abundance and added an interaction term for date and female numbers. Female numbers are likely to decrease with time as females begin to nest. Following the same procedure as above, a spatial autocorrelation weighting was calculated for the presence only points. The optimal lag distance was found to be 3000m. Initially, Poisson errors were used, however, the residuals and variance were not normal and constant, respectively. Therefore we square-root transformed the response and used Gaussian errors which resulted in normal errors and constant variance.

Results

Surveys

There were a total of 160 observations holding three (or more) male Great Bustards. The mean number of mature males at a display site per observation was 9.5 ± 0.4 males (SE unless stated otherwise, range 3 - 29), and the mean number of females at a display site was 7.9 ± 0.7 females (range 0 - 36). The largest mixed sex group was 56, an estimated 40 % of the HNP's population in a single gathering.

The display sites were non-randomly distributed within the national park (nearest neighbour: mean observed = 165.9 m, mean expected = 1050.9 m, z = -31.3, p < 0.01), and mainly found in the southern part of HNP (Figure 1). Kernel density estimation with 95 % probability of occurrence, estimated that two lekking concentrations exist in the southern part of the park, covering 67 km^2 and 79 km^2. The centres of the lekking regions were separated by 11 km. They covered a total of 8 % of the surveyed area (study buffer). As there was spatial autocorrelation present in the display sites, we could not use traditional bivariate tests of difference in means. Table 1 describes the data for habitat variables.

Habitat selection

The MAM for habitat selection had two disturbance variables that significantly explained the probability of male Great Bustard occurrence (Table 2). The model indicated that bustards avoided human disturbance. Bustards were more likely to occur far from tarmac roads, and areas with fewer dirt roads. There was no significant difference in the explanatory power of the maximal model and the MAM (ANOVA: d.f. = 6, F = 1.48, $p > 0.05$). The residuals from the MAM displayed no spatial autocorrelation (Moran's I, $z = -0.25$, $p > 0.05$).

The ROC indicated that the MAM fits the data well and explained 96.9 % of the area under the curve (Figure 2a). Independent validation with survey data from 2004 showed that the predictive power was good, correctly predicting 80.7 % of the presence and absence data (Figure 2b). There was no significant effect of disturbance from grazing, or from the remotely sensed variables such as tasseled cap wetness, greenness and brightness (Table 2).

Table 2. Habitat selection model of male Great Bustard *Otis tarda* display sites using presence vs random sites (n = 160 observations). Minimum adequate generalized linear model is provided with binomial errors and controlling spatial autocorrelation with autologistic term. See Table 1 for explanation of variables.

Retained Variables	**Beta**	**SE**	***Z***	***p-value***
Intercept	-5.83	2.18	-2.67	0.007
Distance to road (m)	0.56	0.28	1.99	0.046
Dirtroad density (m/km^2)	-0.14	0.06	-2.27	0.023
Autologistic term	14.89	2.25	6.63	<0.001
MAM deviance				*166.85*

Removed Variables	**Beta**	**SE**	***Z***	***p-value***	**Order of removal**	**ΔDeviance†**
Distance to cattle (m)	-0.19	0.10	-1.90	0.058	6	3.42
Distance to sheep (m)	0.24	0.13	1.81	0.071	5	4.00
Distance to settlement (m)	0.27	0.42	0.65	0.516	4	0.48
TasCap wetness	-0.01	0.01	-0.59	0.557	3	0.35
TasCap brightness	-0.01	0.01	-0.44	0.660	2	0.19
TasCap greenness	-0.01	0.02	-0.94	0.528	1	0.41
Maximal model deviance				*158.00*		

†**The change in deviance caused by the removal of the variable from the preceding model.**

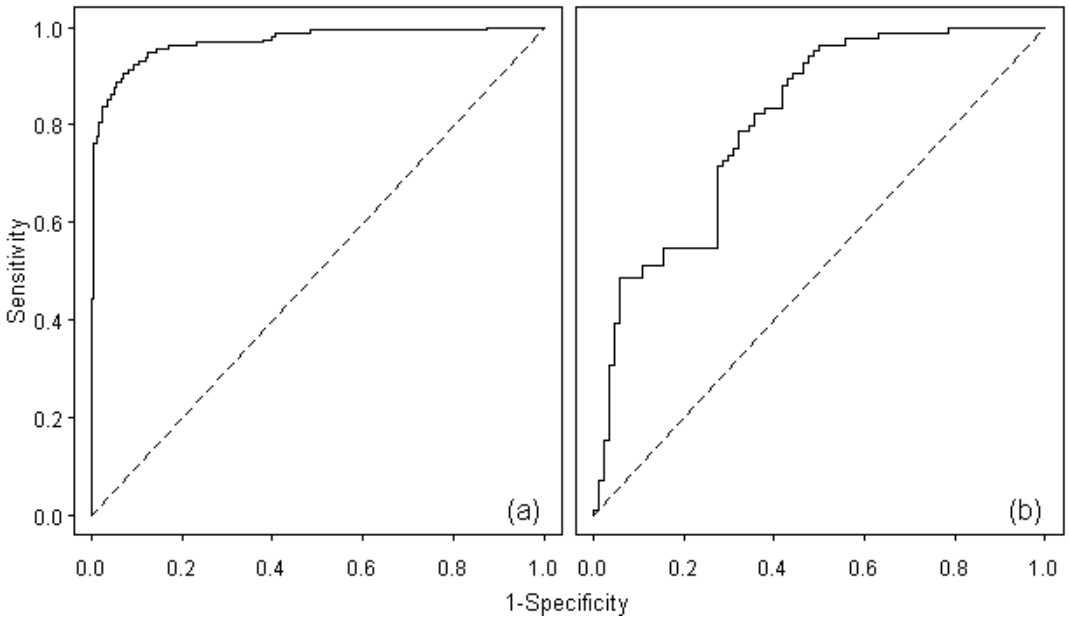

Figure 2. Receiver Operating Characteristic (ROC) plots for Great Bustard habitat selection minimum adequate model to the data (a), and a validation plot (b) for survey data from 2004 not used in the analysis.

Number of males

Distance from roads and dirt road density were included in the maximal model. After simplification, the MAM indicated that there was a strong positive correlation between the number of males and the number of females indicating the importance of social effects on display site attendance (Table 2, Figure 3). Disturbance and habitat features within the male display sites had no significant effect on the number of mature males attending (Table 2) and there was no significant loss of explanatory power by maximal model vs. MAM (ANOVA, d.f. = 4, F = 0.44, *P* = 0.78). There was no spatial autocorrelation in the residuals of the MAM, (Moran's I, z = 0.64, p > 0.05).

Table 3. Predictors of number of male Great Bustards attending a display site (response variable, n = 160 observations). Minimum adequate generalized linear model with Gaussian errors and controlling spatial autocorrelation with autologistic term.

Retained Variables	**Beta**	**SE**	***t***	***p-value***
(Intercept)	2.53	0.10	24.05	<0.001
Autologistic term	0.02	0.02	0.85	0.397
No. of females	0.19	0.03	6.77	<0.001
MAM deviance			*92.90*	

Removed Variables	**Beta**	**SE**	***t***	***p-value***	**Order of removal**	**ΔDeviance**[†]
Dirtroad density (m/km2)	-0.04	0.04	-1.02	0.308	4	0.54
Julian Day	-2.74×10^{-3}	3.97×10^{-3}	-0.69	0.491	3	0.25
Distance to road (m)	0.08	0.16	0.49	0.628	2	0.12
No. of females*Julian Day	-3.44×10^{-4}	2.19×10^{-3}	-0.16	0.876	1	0.01
Maximal model deviance			*91.98*			

[†]**The change in deviance caused by the removal of the variable from the preceding model.**

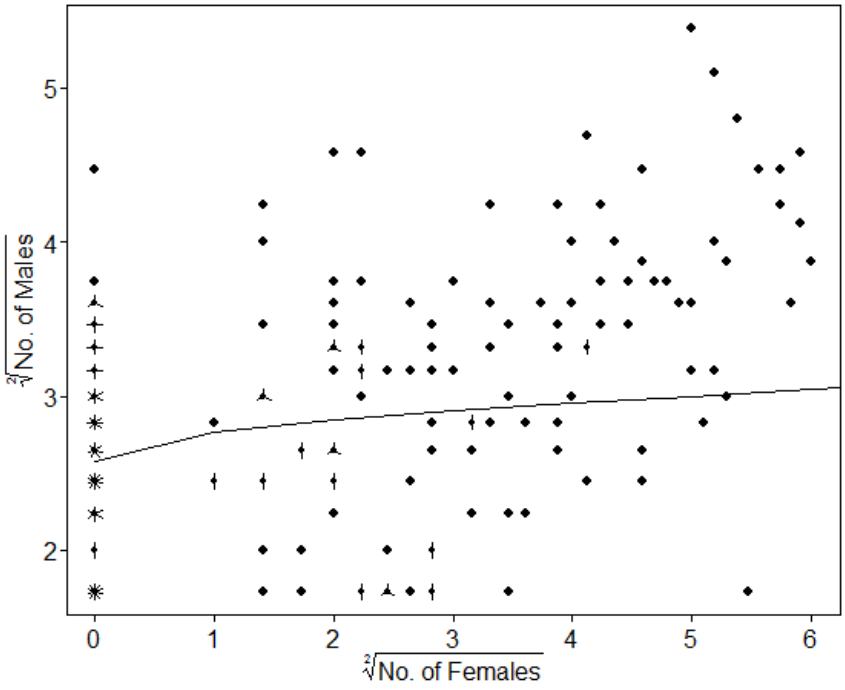

Figure 3. The number of male Great Bustards in relation to the number of females, and the predicting model (continuous line). Petals on the datum indicate sample sizes.

Discussion

Differentiating between presence and attendance can give important insights into the mechanisms of habitat selection. We provide models of Great Bustard habitat preference and we examine the role of additive aggregation for determining attendance at sites. We found that male Great Bustards avoid human disturbance, and that variation in the number of males attending a display site was strongly correlated with the number of females. These results have implications for bustard conservation.

Great Bustards have a lek breeding system and consequently spatial autocorrelation and lek inertia (extreme site fidelity) are potential problems when studying habitat selection (Augustin *et al.* 1996, Lane *et al.* 2001, Osborne *et al.* 2001). Incorporation of spatial weighting allowed us to control for autocorrelation. The term was positive, indicating attraction between the locations of display sites which were likely to be within the 1000m lag distance of each other. Conversely, there was no spatial autocorrelation in the number of males attending display sites. This suggests that individuals were not simply congregating on traditional sites or close to them, but that numbers were dynamic across the large lekking areas. Therefore, lek inertia was unlikely to affect our interpretation of the attendance (Lane *et al.* 2001, Gray *et al.* 2007).

Great Bustards chose displays sites farther from roads than expected by chance indicating avoidance of disturbance. This agrees with our *a priori* expectation as the negative impact of roads and the direct effect of anthropogenic activities have been seen in other populations (Lane *et al.* 2001, Suarez-Seoane *et al.* 2002, Sastre *et al.* 2009). The bustard family, *Otididae*, seem to have a predisposed vulnerability to disturbance, probably due to their predominantly terrestrial life history and ground nesting (Garcia *et al.* 2007, Gray *et al.* 2007, Dutta *et al.* 2011). Non-lethal anthropogenic disturbance caused by roads is a growing concern for conservationists as they can cause anti-predator behaviours such as fleeing, and may carry fitness costs (Miller *et al.* 1998, Goss-Custard *et al.* 2006, Cresswell 2008). Further, excessive disturbance may even lead to complete avoidance of otherwise suitable areas and ultimately altering space use and available habitat (Morales *et al.* 2006, Garcia *et al.* 2007, Speziale *et al.* 2008). This can be particularly acute for species with complex breeding systems or species that congregate to breed (Carney and Sydeman 1999, Manor and Saltz 2003). Human disturbance is an important consideration when managing or planning conservation for or a species.

The number of males was strongly correlated with the number of female Great Bustards and not with disturbance. Positive correlation of males and females on display sites has been found in other lekking species, such as, the Ruff *Philomachus pugnax*, Black Grouse *Tetrao tetrix* and Sage Grouse *Centrocercus urophasianus* (Bradbury *et al.* 1989, Alatalo *et al.* 1991, Höglund *et al.* 1993). Three hypotheses have been advanced to explain the behaviour that leads to these aggregations. Firstly, the hotspot hypothesis suggests that males will congregate on areas where

there are highest concentrations of females or overlapping female home ranges (Bradbury *et al.* 1986). Secondly, the hotshot hypothesis suggests dominant males will attract sub-dominant males which aim to parasitize successful males (Beehler and Foster 1988). Thirdly, female preference for larger aggregations of males may provide greater opportunities for comparison. Proving causality and exclusivity of these hypotheses has been problematic as cause and effect cannot be separated (Höglund and Alatalo 1995). However, behaviours that lead to aggregation are unlikely to be mutually exclusive and will likely operate with feedbacks. For example, overlapping female home ranges may initiate a display area which is visited by dominant males, thereby attracting subdominant males. Then females from other areas may also visit the larger congregation of males. Nevertheless, there is evidence that the probability of finding either sex is increased with the presence of the other.

Behaviours that lead to aggregation through influencing habitat choice can have important implications for population dynamics and species management. For example, conspecific attraction positively influences juvenile dispersal and in turn spatial meta-population dynamics of Great Bustards (Alonso *et al.* 2004, Martin *et al.* 2008). Similar patterns are found across a broad range of animal taxa, including lizards, birds and mammals (Stamps 1988, Hoeck 1989, Weddell 1991, Gautier *et al.* 2006). The influence on population dynamics can lead to aggregation of territories, empty suitable habitat empty and increased extinction risk of patches (Ward and Schlossberg 2004).

Beyond considerations of habitat management, conspecific attraction could be used to actively manipulate spatial distribution for conservation purposes (Ahlering *et al.* 2010). Experimental studies have shown that site selection can be influenced using decoys and calls to simulate conspecific presence (Doligez *et al.* 2002, Ahlering and Faaborg 2006, Parker *et al.* 2007, Kappes *et al.* 2011). For instance, Jiguet and Bretagnolle (2006) demonstrated that Little Bustard *Tetrax tetrax* lek location, the number of individuals attending it and the composition of individuals, could be manipulated with the use of decoy conspecifics. Furthermore, decoys have been successfully used to aid recolonisation of empty habitats for colonial seabirds (Parker *et al.* 2007, but see Oro *et al.* (2011)). Smith & Peacock (1990) highlighted the importance of considering conspecific attraction in reintroductions because the probability of utilizing unoccupied suitable habitat is low, leading to a small number of occupied patches. Although we are not aware of formal testing, Great Bustards have been known to respond to decoys during hunting (Sowerby 1914), and although at an early stage, there has been promising use of decoys to influence the display sites of males in the UK Great Bustard reintroduction trial (pers. obs.).

We found no effect of human disturbance on the number of male Great Bustards. We suggest two explanations for this. Firstly, the sites where Great Bustards occur were already high quality or at least minimally suitable for occupancy. It is likely that when a minimum threshold of tolerance is

reached, decreasing disturbance has no bearing on the perceived quality of the habitat. Because the number of Great Bustards was not explained by heterogeneity in disturbance, abundance may be a misleading metric for habitat quality in Great Bustards or other social species (Vanhorne 1983, Stamps 1988, Skagen and Adams 2011). Strong conspecific attraction suggests that Great Bustards are vulnerable to an "ecological trap", whereby individuals remain faithful to a sub-optimal site and dispersing individuals select a site based on their presence (Székely 1992, Schlaepfer *et al.* 2002, Patten and Kelly 2010). Secondly, our proxies of human disturbance may not have captured the correct biological component. We cannot fully discount this argument, although note that human disturbance was important in influencing the probability of occupancy.

Validity of habitat selection results

It is important to carefully interpret habitat selection results for species living within a national park because features outside or far from the park would be negatively correlated with species occurrence simply because they are not in the park rather than actively influencing the species distribution. Therefore, we must determine whether the features are meaningful for the species' habitat choices or simply a chance correlation with some unmeasured meaningful factor.

In this analysis, the majority of the display sites were within the park or just outside the park boundary. Whereas, many settlements and tarmac roads were predominantly outside the park, although dirt tracks were found consistently throughout the whole study area. Therefore two possible scenarios arise: 1) the features are meaningful and the park is chosen by great bustards because of the absence or low occurrence of these features, or 2) another unrecorded feature within the park is being chosen and the park just happens by chance to have few settlements or roads. For example, nesting areas may be intensively managed within the national park but not as intensively outside leading to a greater productivity in the park and increasing the occurrence of birds, or again, fewer pesticides are used in the park than outside leading to a greater abundance of invertebrates in the park during the breeding season. Hence, the lack of disturbance in the park may not be the feature bustards are selecting, but simply it is correlated with other the other features of the park which the birds are choosing.

In this study, it is likely the variables are meaningful as they were not chosen at random and we had pre-existing evidence to support the importance of disturbance in great bustard habitat selection. Particularly, great bustards' exhibit a strong flushing behaviour when disturbed by humans or vehicles. While the evidence supports our a priori theory, we cannot fully discount the possibility that other unmeasured variables could remain important.

Conclusions

Here we found that human disturbance influences the spatial distribution of display sites although the abundance of males at a display site was best predicted by the number of conspecific females.

Social cues are undervalued in conservation biology, and are not typically incorporated into habitat selection models (Fletcher and Sieving 2010). For the Great Bustard, which is experiencing habitat loss throughout its range and increasing fragmentation, the restoration of unoccupied habitats may prove futile, if the probability of colonization is low. On-going and proposed reintroductions of the Great Bustard could potentially use conspecific attraction to manipulate habitat choice and to open up new habitats. Our study therefore adds to the growing evidence supporting the role of conspecific attraction in habitat choice and highlights its significance in conservation.

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Supplementary Material

Appendix Table S1. Landsat ETM+ scenes used to create Tasseled Cap Transformations for Hortobágy National Park.

Acquisition Date	Path	Row	Scene ID
23/04/2000	186	27	LE71860272000114EDC00
25/03/2001	186	27	LE71860272001084SGS00
20/04/2002	187	27	LE71870272002110SGS00
16/04/2003	186	27	LE71860272003106ASN00
20/03/2005	186	27	LE71860272005079ASN00
05/04/2005	186	27	LE71860272005095ASN00
24/04/2006	186	27	LE71860272006114ASN00
08/04/2006	186	27	LE71860272006098EDC00
26/03/2007	186	27	LE71860272007085ASN00
27/04/2007	186	27	LE71860272007117EDC00
02/04/2007	187	27	LE71870272007092ASN00

Appendix Figure 1. Frequency histograms variables representing human disturbance and vegetation structure were obtained via remote sensing for presence sites, *n* = 160, and randomly chosen sites, *n* = 160.

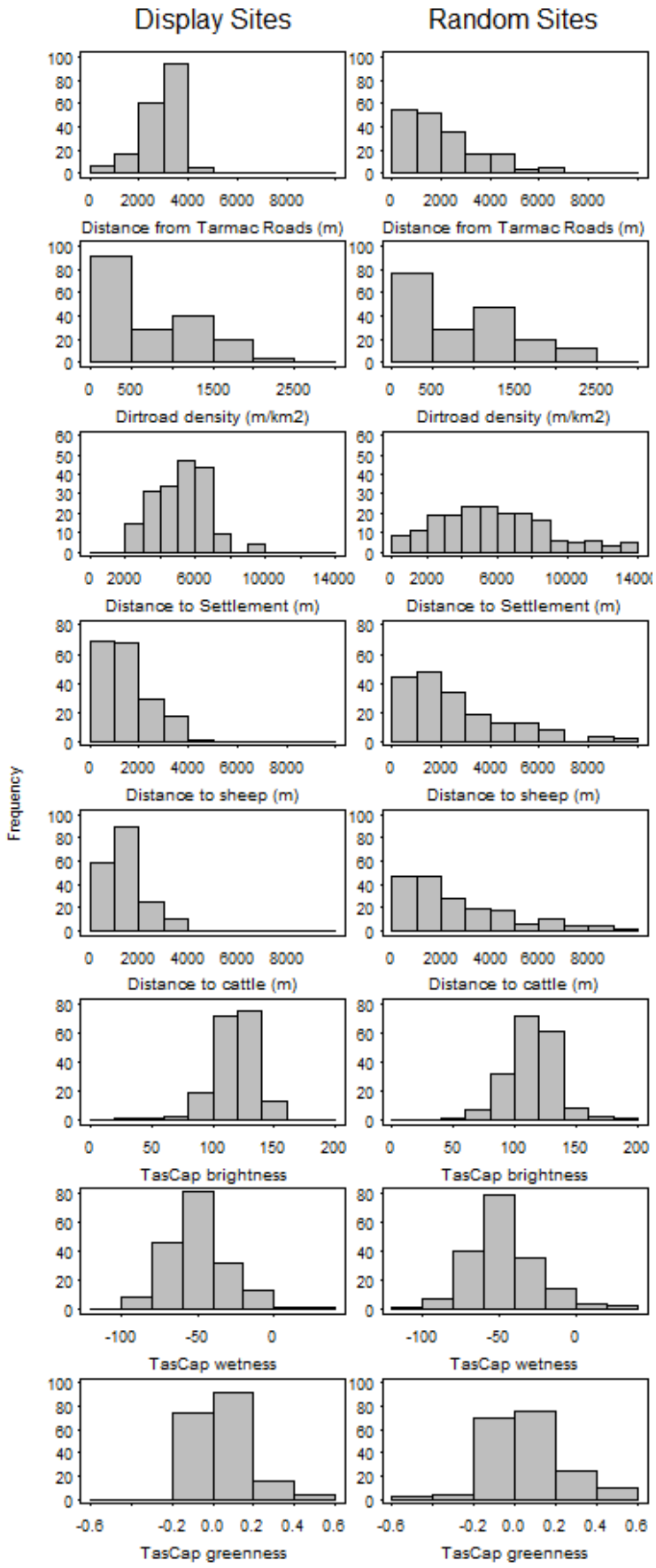

Image 7. Male Great Bustard, Purple 5showing aggression towards another male bird at the release site on Salisbury Plain. Photograph by John Burnside.

Chapter 6: Conclusions and future directions

Robert J. Burnside

Overview

In this thesis, I have presented and contributed knowledge of the factors affecting the establishment of a reintroduced threatened species, the Great Bustard *Otis tarda* in the UK. Additionally, I presented results from an observational study of the roles of disturbance and social cues in breeding site choice and attendance. The main results are as follows:

- The estimated survival of captive-reared Great Bustards is substantially lower than wild counterparts. Mortality is highest during the six months after the release and mainly caused by predation and collisions with fences and powerlines.
- There is a significant improvement in survival after the first six months of release with captive-reared adult Great Bustards having comparable, even if slightly lower, survival to wild counterparts.
- Population modelling suggests that if current reintroduction efforts continue "business as usual", the founder population will remain small and unlikely to grow. Since the reintroduction project has so far not produced young that recruited to the population, improving breeding success will be another task to achieve a viable population.
- The date of release influenced survival during the first six months after release. Releases in September produced individuals with a higher survival probability than those released in October.
- Reintroduced Great Bustards traversed large areas, but showed multimodal distribution of distances travelled. All birds incorporated the release site into their range. There was little evidence of post-release effects on dispersal with only 5 individuals' under-going unusually long distances greater than 100 km from the release site after release.

My PhD sought to address the conservation management of a single species with a scientific and pragmatic approach. Therefore, it contributes to the conservation biology of the Great Bustard. Although superficially the results may only appear applicable to the formerly mentioned system, they may have broader implications for the fields of reintroduction biology, behaviour and habitat selection.

Establishing founder populations

The ultimate goal of a reintroduction is to create a self-sustaining population, however, a simplistic binomial variable of success or failure often does little to identify the true processes determining the outcome. Similarly, highly variable definitions of success also reduce our ability to draw comparisons between projects (Seddon 1999). Rather, splitting the reintroduction into biologically

meaningful stages, and assessing the relevant factors influencing these stages, can yield comparable insights.

Armstrong and Seddon (2008) proposed a key question of the population establishment process is understanding the influence of pre and post-release management on post-release mortality and dispersal. Chapters 2 – 4 address this issue directly whereas Chapter 5 addresses it indirectly and has implications for reintroduced as well as extant population persistence.

Founder population projections

In Chapter 2, I used population modelling to show that low post-release survival and release numbers would limit the size of the UK Great Bustard founder population. Population modelling allows for exploration of variables that affect population growth (Boyce 1992). Although building a model can be a useful thought experiment, population models often only give meaningful insights when parameters estimates are reliable (Beissinger & Westphal 1998; Boyce 1992; Caughley 1994). This was demonstrated by how optimistic with the original model projections were during the feasibility stage of the UK Great Bustard reintroduction (Burnside et al. 2012; Osborne 2002, 2005). Whereas, the revised projections remain accurate in 2012 with the deterministic model predicting 10 individuals by 2012 and 5 – 30 individuals from the stochastic model (Chapter 2). The current confirmed population size of birds greater than one year old in 2012 is nine (Ashbrook, *pers. comm.*).

This emphasises why estimating life history parameters remains one of the most important steps in reintroduction biology. This is particularly true for the measurement of "*post-release effects*" (Armstrong & Reynolds 2012). These effects are described as a period of time after release when there are changes in vital rates, such as survival or dispersal, due to the stress of release and the period needed for acclimatisation. Tavecchia et al. (2009) called this the "*cost of release"* and defined a method to quantify the cost. This method was not employed here because it is based on assumptions about released individuals which are not met in this reintroduction. However, the recognition and incorporation of post-release effects remains important for reintroduction management. These effects have been described for post-release survival and dispersal in birds, mammals and plants (Biggins et al. 2011; Godefroid et al. 2011; Hardman & Moro 2006; Mitchell et al. 2011; Nicholls & Pullin 2000). For these reasons, in Chapters 2 – 4, I investigated various aspects of survival and dispersal of Great Bustards revealing post-release effects on survival but few on dispersal. Both factors can be important management problems and must be considered in reintroductions.

Low founder population recruitment

Low survival and low release stock numbers are a hurdle for creating a founder population. Although increasing recruitment through releasing more individuals is an option, the ethical and

overall better option for bustard conservation is to improve survival capability in captive-reared individuals. However, there is still a large gap in our knowledge of why captive-reared animals are so vulnerable to mortality and the mechanisms by which they acquire the correct behaviours for survival in the wild (Dickens et al. 2009; Griffin & Blumstein 2000; Wallace 2000).

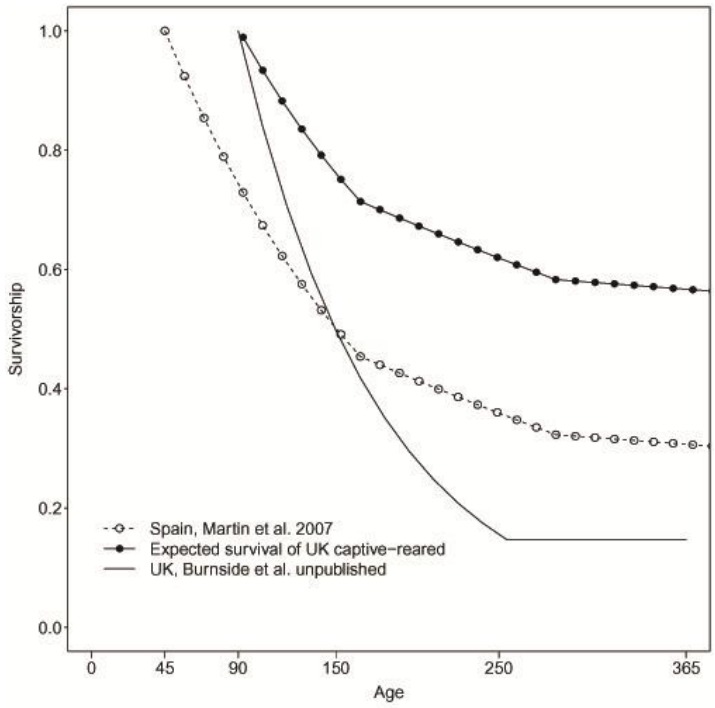

Figure 1. Survivorship curves for Great Bustards released in the UK and wild Great Bustards from Spain. The expected survivorship curve of Spanish birds of similar age to reintroduced individuals shows large difference in the expected survival or wild individuals. UK birds are released around the age of 90 days old.

Captive-reared Great Bustards have a similarly high vulnerability to post-release mortality as do many other captive-reared species (Chapter 2 & 3). Numerous case studies have noted higher mortality in captive-reared or captive-bred animals compared to wild-reared conspecifics within the same population, such as white-tailed eagle *Haliaeetus albicilla* (Evans et al. 2009). Furthermore, meta-analyses within groups, like carnivores, have shown that the pattern is consistent across projects and species (McCarthy et al. 2012). The pattern raises questions about the ethics or appropriateness of using captive-reared animals in reintroductions when a large proportion of individuals are "*doomed to die*". Although, there have been exceptions where captive-reared individuals have similar survival to wild released conspecifics, such as in the Mauritius kestrel *Falco punctatus* (Nicoll et al. 2004). Ironically, the implementation of many reintroductions are

thought to be motivated by the existence of an excess of captive-bred individuals rather than by a well thought out conservation strategy (Seddon et al. 2007).

We cannot make direct comparison with the survival of wild translocated Great Bustards because I am not aware of any that have ever occurred. Although the comparison to wild individuals is confounded by different environments, it remains our best gauge by which to measure the negative effect of captivity or reintroduction stress on survival. The best example of Great Bustard survival data exist from the Spanish population, and these wild birds experience high mortality but not to the same degree as the captive-reared birds (Martin et al. 2007). UK Great Bustards are estimated to have 10 % surviving from 2 - 8 months old compared to 60 % for peers in Spain (Fig. 1). Unfortunately, there is little output from the Hungarian release project and few detailed analyses from the German projects with which to make comparison. However, that said, high mortality and predation are known to be a significant problem for these supplementation projects.

Low survival management interventions

First, as post-release mortality is often caused by predation, the most common management strategy is to reduce the contact with predators, with measures like predator control, and predator-free areas. However, this is likely to treat the symptom rather than the cause and may not offer a long-term solution. Simply removing contact with predators may only delay mortality rather than addressing the real issue of behaviour. For example, displacement of predators in houbara bustard *Chlamydotis undulate* releases simply changed the temporal and spatial component of mortality but survival ultimately remained the same (Combreau & Smith 1998). The UK project utilises a predator free release pen and limited fox control, but still experiences high mortality. The German and Hungarian projects have had similarly low success with post-release management of captive-bred birds through predator free pens and predator management (Eisenberg 2008). Therefore removing contact with potential predators does not present a convincing solution.

Secondly, the results of Chapter 3 indicate that the mortality rate can in part be mitigated by release techniques. Particularly, releasing individuals in August or September is preferential to October and could improve the survival rate to 6 months after release from 1% to 20 %, respectively. However, I was unable to explain definitively the cause of this variation. In the Chapter, I discuss potential explanations, for example, seasonality, increasing time in captivity and reduced ability to learn with time. Equally, because collisions were a common cause of mortality it has been suggested that the increased time in quarantine causes a cumulative reduction in feather quality due to abrasion with netting and the need to handle birds. Unfortunately, feather quality was not always recorded in the past and this hypothesis cannot be formally tested, yet. Although, from my experience birds can show heavy signs of damage and loss of tail feathers before release. Realistically, mortality is a complex matter and every factor would additively contribute to the vulnerability of Great Bustards. Many release procedures did not have an effect of survival, for

example, group size and sex of the individuals did not contribute to individual variation in survival (Chapter 3). Currently, there is a 40 % difference in mortality between the Martin et al. (2007) estimates and the UK birds (Fig. 1). Hence, there is much variation that remains unexplained.

Thirdly, a future area for experimentation will likely be with pre-release management. Particularly, there are three areas: predator awareness training (PAT), parental replicated rearing conditions (PRRC) and reducing accumulated stress. PAT has been discussed extensively during the project, however, the difficulties of implementing the procedures has raised doubt of its usefulness. Previous attempts at PAT in 2005 did not present any striking results with equal survival rates between two treatment groups (Burnside, unpublished data). However, refining the techniques could produce different results. Positive results have been reported with captive-reared houbara bustards that showed a significant improvement in survival with predator training using a live fox. However, the practice remains debatable as birds can be injured during the process (van Heezik et al. 1999). The trade-off between losing birds during training, in exchange for improved survival in some birds after release, is a challenging decision to make. Overall, the evidence supporting PAT in birds is still equivocal (Fischer & Lindenmayer 2000).

PRRC and reducing stress presents an interesting option for improving behaviour in birds. However, they may be difficult to implement in a project such as this due to the complex process of rearing in Russia, long distance transport, quarantine and multiple handling sessions before release. Cumulatively, this increases the chances of trauma injuries occurring, damages feathers, potentially habituates individuals and may cause cumulative stress on the individuals during release. All these are currently unavoidable with the reintroduction methodology. These can be addressed by rearing chicks in the UK or identifying closer source populations which are not subject to the same restrictions as birds from Russia. Currently the Great Bustard Group is trialling egg transport and rearing in the UK.

This is an area that requires substantial amounts of future research. However, implementing research on these areas presents many difficulties due to the unpredictable nature of egg rescue and the long-time frames over which it must be carried out.

Long distance movements

Great Bustards showed an astounding ability to move around the UK and beyond (Chapter 2 & 4). As mentioned in Chapter 4, these movements have mixed consequences for the reintroduction. On the positive side, movements show that individuals are able to locate habitat around the UK and allow us to identify areas that may be suitable for the species. On the negative side, it brings added difficulties to managing the population as birds move to areas that may not be managed. Furthermore, as the distances covered are large, it reduces our ability to monitor individuals, particular for habitat choice. Therefore, in the future it is not important to limit the movement of the birds but rather increase the ability to monitor the birds beyond the release site. Currently,

controlling movements does not present a priority management task for the establishment of a founder population as surviving individuals show fidelity to the release area.

The estimates of true dispersal rates are confounded by high mortality as many birds died before they got a chance to undertake dispersal. Conversely, some birds that I classified as permanently dispersed may also have died before gaining the opportunity to return. Although these estimates may have debateable biological meaning, they represent our best current understanding for predicting what will happen if we continue to release birds under the same system. Improving dispersal estimates will only be addressed through the continued monitoring of birds that survive beyond the post-release mortality period. Further, this advocates the need for the current UK project to incorporate dispersal targets into the population management plan.

Habitat and behaviour for conservation

There is an increasing acceptance that animal behaviour can inform conservation management (Caro 1999; Sutherland 1998). In Chapter 5, I investigated Great Bustard habitat selection and its behavioural influences. I showed that the variation in females predicts the number of males attending a site rather than the variation in distance from roads. It remains that disturbance is an important factor in Great Bustard habitat selection and indeed has been confirmed in other studies (Osborne et al. 2001; Sastre et al. 2009). However, this is not a factor that worries me greatly for the UK population. It is likely that flexibility in behaviour is limited when species have overlapping generations and transfer behaviours, analogous to the "*ecological trap*" (Schlaepfer et al. 2002). For example cranes *Grus grus* show consistent avoidance of disturbance in summer and wintering areas depending on which population they originate from (Végvári et al. 2011). This means that if you grow up near a disturbance, you will have a consistent tolerance to that disturbance in future.

Ultimately, roads are a non-lethal disturbance to bustards and if individuals are habituated to the disturbance it is unlikely to cause a significant impact on the animal. Great Bustards have been shown to socially transfer migration routes and show high fidelity to natal areas (Martin et al. 2008; Palacin et al. 2011). If the passed-on behaviours are avoidance of disturbance, then hypothetically, the behaviours that favour habituation to disturbance will be passed on in the UK. Thereby, we could surmise that captive-reared animals are better for a new environment as they may be the proverbial "*blank slate*" upon which to draw. Conversely, translocated wild adults from other populations, like Hungary and Russia, may not adapt well to the UK habitat.

Reintroductions depend on finding suitable habitat or establishing individuals in the area with suitable habitat. Integrating understanding of conspecific attraction and habitat selection could allow for managers to manipulate the habitat choices of the target species in a reintroduction or conservation setting. This also will allow experimental manipulation through the use of decoys. Anecdotally, we have seen responses of reintroduced Great Bustards to decoys (pers. observation); however, these observations are confounded because they occur at the release site and therefore do

not represent a truly independent choice. Conspecific attraction is likely to be the reason for all the surviving Great Bustards incorporating the release site into their home ranges (Chapter 4). The presence of other individuals and experiencing the presence of other individuals will have anchored them to the site.

Population Persistence

As of yet the quantification of breeding productivity and survival for wild-born individuals remains undone. As the species is very long-lived and low fecund, this will be a long-term goal. For example the natural invasion of *Grus grus* to Norfolk only successfully fledged six chicks over 20 years with positive but slow population growth (Mathews & Macdonald 2001). This will likely be an important avenue for research in the future and accordingly the reintroduction project has designed targets for survival and productivity (Burnside & Carter 2010).

This research highlights the limitations of the establishment phase of the reintroduction but does not give insight into the potential persistence of the population. I chose not to incorporate breeding or survival of wild-reared individuals because the data did not exist. Although it may still be premature to carry out a full Population Viability Analysis (PVA), when the data become available their application will prove important to the reintroduction. They provide an excellent means of testing scenarios, especially when resources are limited (Brook et al. 2000). For example, Green *et al*., (1996) used modelling to simulate a reintroduced population of white tailed eagle had a high probability of extinction unless there was further supplementation. Schaub *et al*., (2009) used modelling to show that a reintroduced population of bearded vultures *Gypaetus barbatus* would maintain positive growth and no longer needed further releases. This motivated the decision to divert valuable resources to increase monitoring and to use captive stock for other reintroduction projects. Conversely, Meretsky *et al*., (2000) used modelling to set the target survival rates for Californian condor *Gymnogyps californianus* reintroduction and found that survival of released individuals was below that needed to have a stable population. Therefore they suggested halting releases until the issues causing mortality could be addressed.

Since reintroductions of many species are either one-off events or first attempts to reintroduce the species, modelling remains the most appropriate method for understanding the influence of life history parameters on population level dynamics (Armstrong & Reynolds 2012).

The role of reintroductions in bustard conservation

Reintroduction Feasibility

The results presented here are only a small part in the steps needed to ensure a successful reintroduction. We have found limitations that are by no means unique to the UK project. Overall, these limitations are not a guarantee that Great Bustards would fail to persist in the UK.

Particularly, high post-release mortality does not indicate that UK habitat is unsuitable for population persistence. I reach this conclusion for two reasons:

First, it is important to keep in mind that reintroduced populations can fail to establish even in conditions that would otherwise allow persistence. This has been demonstrated several times in reintroductions that were close to failure but changes in strategy allowed successful establishment and subsequently populations have increased to carrying capacity and persisted, such as the Mauritius kestrel *Falco punctatus* and pink pigeon *Columba mayeri* (Jones & Merton 2012).

Second, both supplementations in Germany and Hungary which release captive-reared birds, have high post-release mortality (Eisenberg 2008). Regardless, both countries have existing populations that continue to persist albeit with conservation habitat management. This indicates that the high mortality of captive-reared birds is not reflective of unsuitable habitat but rather the unsuitability of captive-reared bustards for release. Indeed, at best with the current methods the UK project would expect to replicate the slow growth of the German project, which with 20 years of rear and release, has seen an increase of around 50 individuals, a doubling of the population.

The reintroduction is potentially feasible but the reintroduced populations will likely remain small and take a long time to grow. The current adult population and the estimated adult population at the end of the trial in the UK would have a decreased probability of persisting simply because it is small and susceptible to demographic stochasticity and catastrophic events (Caughley & Gunn 1996). Furthermore, since the population will be focused on one central population and release site, it will be particularly susceptible to catastrophe through parasites and disease (Ewen et al. 2012). These are important management considerations for the reintroduction.

Twelve out of 26 bustard species are classified as near threatened to critically endangered (IUCN 2012). Three of the species are critically endangered/endangered, including the great Indian bustard Ardeotis nigriceps, Bengal florican *Houbaropsis bengalensis*, lesser florican *Sypheotides indicus* (Dutta et al. 2011; Munjpara et al. 2011). Captive-breeding and reintroduction or supplementation are suggested as possible conservation strategies for these species. Based on the evidence of this and other projects, it is likely that attempts will struggle to make a real impact without a clear and abundant stock for release. So far, captive-breeding attempts have not been overly successful in bustards, with the exception of the middle Eastern effort to captive-breed houbara bustards on an industrial scale for hunting. Also, Kori bustard *Ardeotis kori*, Australian bustard *Ardeotis australis*, buff-crested bustard *Eupodotis rufricrista gindiana* and white-bellied bustard *Eupodotis senegalensis* have been successfully bred in zoos but have never been released to the wild that I am aware off (Hallager 2012). However, these are usually in such low volumes that they do not present viable prospects to aid reintroduction, for example, around 111 kori bustard have been hatched in captivity since 1988 (Hallager 2005; van Heezik et al. 1999; Ziembicki 2010).

Any future reintroductions must balance the need for release stock and any post-release effects on dispersal or mortality. The UK Great Bustard project is the first true reintroduction of the

species. As such, much of the lessons learnt are pioneering and it is likely that post-release results can be improved through continued research and adaptive management.

Monitoring in reintroductions

The use of monitoring data was vital in providing accurate measures to assess the progress of the reintroduction. The culmination of analysis from Chapters 2 - 4 are from data acquired during long-term post-release monitoring of marked individuals released as part of the project. The IUCN reintroduction guidelines were consulted during the feasibility study phase of the project and these guidelines have proved important for addressing many areas of possible failure. Monitoring has been essential in allowing the assessment of causes of mortality, estimation of vital rates and movement.

There were limitations to the estimates of life history traits with CMR because it is built on various assumptions of monitoring design, such as, finite resighting phase that is shorter than the non-resighting phase (Lebreton et al. 1992). Monitoring in the UK reintroduction was not designed with this objective but rather as a near continuous monitoring effort at the release site. This is in part due to the long-term nature of the project which during its growth had changing scientific partners. Therefore, post-hoc segregation of the data was necessary to meet assumptions of the models. Although it is unlikely to be a problem this highlights that the monitoring was not systematically designed throughout the entire period to date, a problem is seen in many reintroductions.

The role of different monitoring methods has been contentious within the reintroduction and there is often a cost-benefit trade-off (radio-tags vs GPS devices). Even so, the project has shown that with a charismatic and unique species, sightings by the public can be a useful source of information. Although, this data is not systematic and has unpredictable reporting rates. Unfortunately the high mortality rates of birds has meant that few individuals with tracking devices have been available for study and majority of long-term data off-site has been limited. It is likely in the future the most cost-effective devices will be GSM-GPS transmitters, however, their reliability still remains to be proven.

The role of science in reintroduction biology

How far have we come?

There remains a dichotomy between the practice of science and the management of reintroductions. Particularly, the need to carry out long-term studies potentially with experimental design are often not the objectives of a reintroduction manager (Caughley 1994). Here we have endeavoured to study the progress of the reintroduction and make the results available to the conservation

community. Can it be claimed that science has been beneficial to the reintroduction of the Great Bustard in the UK? Generally, the analysis and dissemination of the results is useful for the conservation, especially when it comes to undertaking feasibility studies, and understanding trends across reintroductions. Unfortunately, or rather realistically, this short-term research project has not found a "*golden bullet*" to address all of the difficulties that a reintroduction faces. In reality, the summation of this PhD represents a link in the adaptive management chain of a reintroduction (Fig. 2). The process is described in McCarthy et al. (2012) and it represents the steps from the first releases, reviewing outcome, identifying problems and using modelling to decide where to invest future resources.

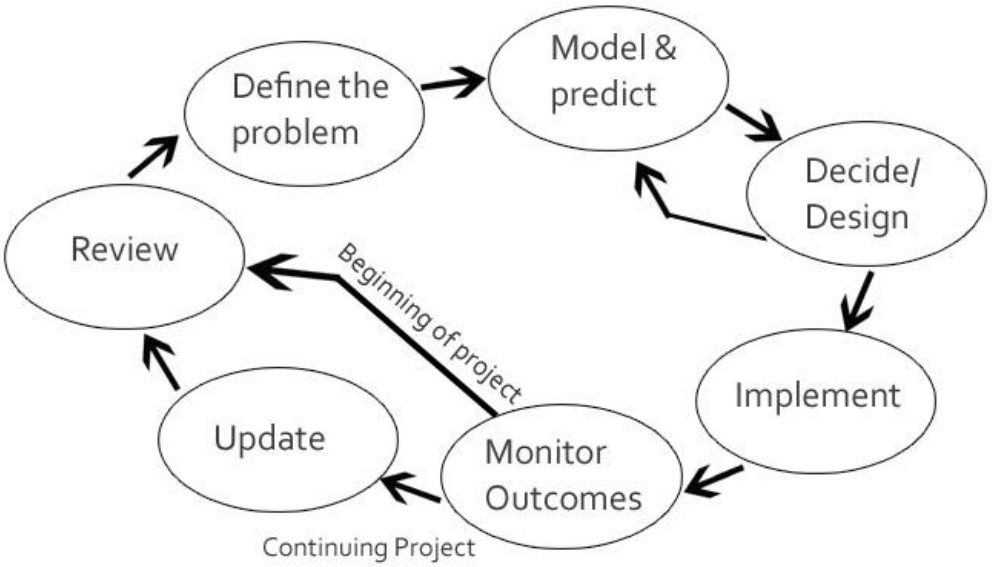

Figure 2. Reintroduction Adaptive Management cycle including the beginning of a reintroduction when preliminary data first become available from monitoring; next techniques undergo review, and problem is defined and projections made; this helps inform decisions which in turn get implemented and the cycle continues. The diagram has been adapted from McCarthy et al. (2012).

Long-term projects are tinged with anecdotes and tricks of the memory as well as political tug-of-wars. Carrying out formal experimental research on these projects is exceptionally challenging due to the constraints of time, low availability of release stock and international transport of birds. Even though the reintroduction in itself is an experimental trial, the results in this research were from *a posterior* analysis and observational in nature. Regardless, I am able to propose refinement of release techniques and therefore it is possible to assess outcomes and

techniques without formal experimental, although it is arguably less powerful (Nicoll et al. 2004). I recommend that in future experimental design of releases remains considered.

Recommendations for conservation actions:

These are some recommendations that I see as important for future management

Pre-release

- Locate additional release stock.
- Experiment with revised predator training.
- Revise quarantine pens to reduce crowding.
- Reduce handling events and time in captivity to improve feather quality.
- Attempt long-term parent substitution with suited humans.

Post-release

- Reduce or remove fences at the release site.
- Add additional release sites within 30 km of existing release sites.
- Continue monitoring to assess the outcomes of treatments and use a control where possible.

Future directions

There are many areas for future study (many discussed above) of the Great Bustard reintroduction and for reintroduction biology. Additionally, two areas where I see a need for further research are discussed below.

Habitat availability & carrying capacity

The future size of the UK population will be dependent on the availability of suitable habitat in the UK. Currently the habitat choice of Great Bustards in the UK remains to be systematically quantified although we know they have preferences for certain agricultural crops. The use of agricultural areas can be beneficial because land can be managed with bustard friendly crops and incentivised from agri-environment schemes. A formal assessment followed by the calculating the area needed to sustain an individual will inform the future of the project. This will allow quantification of the amount of habitat available in the UK and ultimately the carrying capacity. The latter will be the best indicator of the potential population sizes in the UK.

Population Genetics

Reintroduction managers rarely consider population genetics when managing a reintroduction. However, theory predicts that the successive population bottlenecks that conservation reintroduction species pass through will remove much genetic diversity. Further, small isolated populations will be prone to inbreeding and loss of variability through genetic drift (Keller et al. 2012). Inbreeding events may be further amplified in a polygamous species, such as the Great Bustard, when few males are disproportionately successful at breeding. The theory has now been demonstrated in reintroduced populations which show reduced breeding productivity as a result of

lower genetic variability (Biebach & Keller 2010; Robert 2009). The genetic variability in the UK population remains to be quantified although it is underway (collaboration with Paul O'Donoghue, University of Chester), but the theory predicts that this population will be susceptible to a loss of genetic variability. Therefore this will likely be an area for long-term consideration and future research.

Acknowledgements

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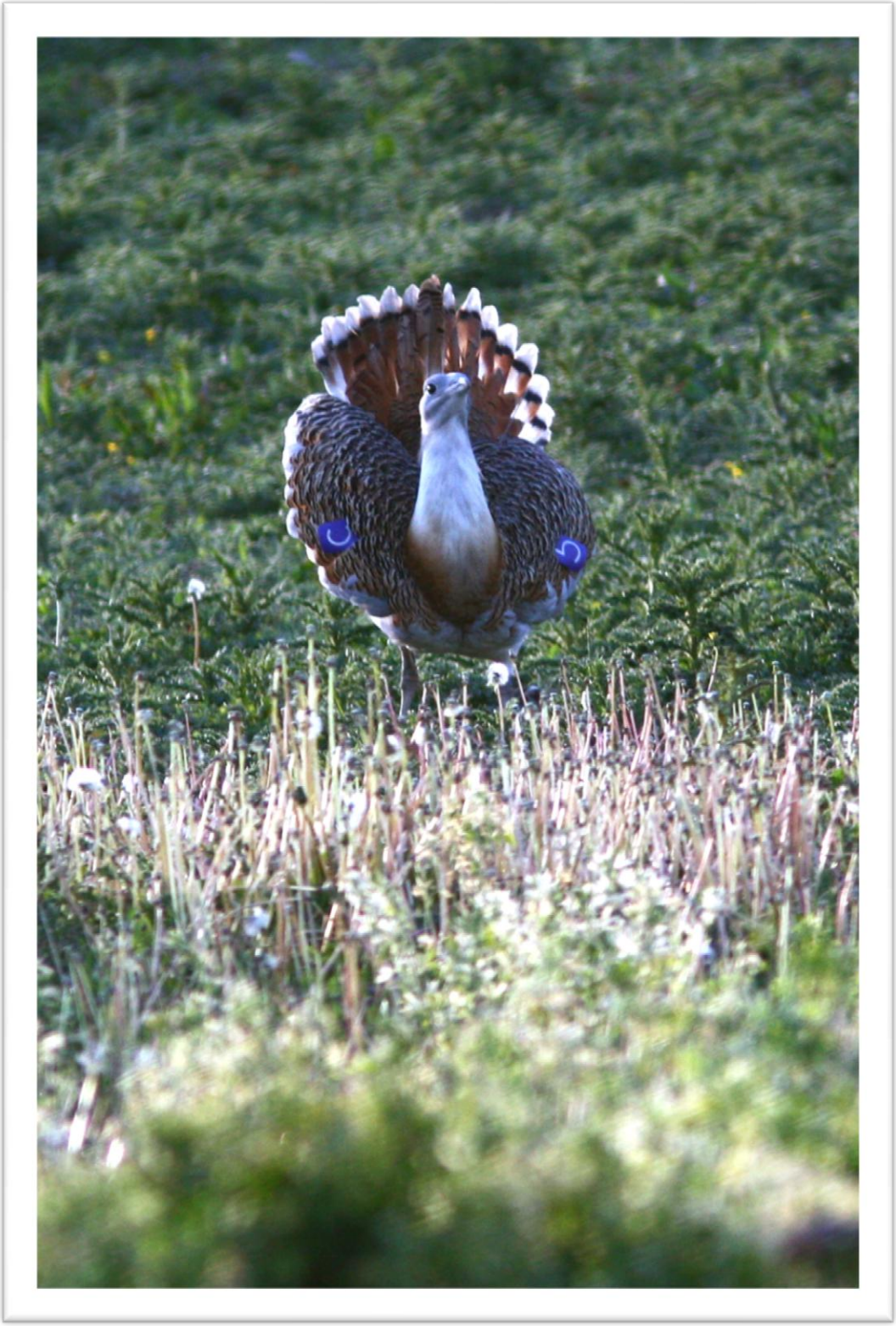

Image 8. The male Purple 5 on the lek preparing to start displaying on a spring morning. Photograph by John Burnside.

Appendix 1: Booming bustard: characterisation of sonate drum sounds during mating displays of the Great Bustard (*Otis tarda*)

R. J. Burnside · J. E. Parra · T. Székely

Manuscript

Authors Contributions

RJB: Recordings, analysis, manuscript

JP: Analysis

TS: Manuscript improvement

Abstract

Bustards (Otididae) are among the most sexually selected bird species as indicated by an extreme range of sexual size dimorphism reported from the 26 species. Studies of mate choice and sexual selection, however, have focused on visual displays in bustards. Here we report the acoustic displays of male Great Bustards *Otis tarda*. We recorded the vocal displays of one male in captivity, and analysed the records using Avisoft SASLab software. Great bustards produced low frequency calls (boom or drum) with a mean frequency 113Hz that last for 0.3s. We propose that these low frequency booms are under sexual selection and target conspecifics: either males or females. Testing the role of these booms in mate choice and male-male competition warrants further investigation.

Keywords *Otis tarda* · Mechanical sounds · Gular pouch · Sexual selection

Introduction

Sexual selection has resulted in the evolution of many secondary sexual characteristics, such as bright colours, ornaments, elaborate displays and acoustic signals. These are considered to be signals of mate quality and therefore have been the focus of evolutionary studies of sexual selection. Extreme examples of the evolution of secondary sexual characteristics are found in polygamous lekking species, of which the Great Bustard (*Otis tarda*) is a prime example.

The display of the Great Bustard is enigmatic, as firstly the males are greater than twice the weight of females, the largest sexual size dimorphism in any bird species (Raihani et al. 2006; Székely et al. 2007). Secondly, the males have various elaborate secondary sexual characteristics: moustache, dimorphic plumage colour and gular pouch. Thirdly, the Great Bustard performs a display ritual in which it inflates its gular pouch, erects the moustache and inverts its wings and tail feathers taking on the appearance of a ball of white feathers. On the lek, males compete for females and there is thought to be a strong skew in mating success with only a few males gaining most of the copulations (Alonso et al. 2010a; Alonso et al. 2010b). Clearly strong sexual selection is occurring in the species, however, exactly which signals are used by males still remains unclear. Several authors have suggested that signals of quality in male Great Bustards is purely visual. For example, females may select older males, who are "bigger", have longer moustache feathers, mature neck plumage, exposed strips of the neck and greater display rates (Alonso et al. 2010a; Alonso et al. 2010b; Gewalt 1959; Johnsgard. 1991; Morales et al. 2003).

However, it has been noted that male Great Bustards have been known to emit a "boom", (also described as an "Umph"), during display. This signal has proved to be controversial – considered by some to be a by-product of the vigorous display during the re-inflation of the gular pouch (Gewalt, 1959). The vocalisation is difficult to hear in the wild and easy to overlook for several reasons. It is only emitted briefly during full displays when the males are in breeding condition during the lekking period. To hear the sound you have to be closer than 50 m and as Great Bustards are shy and prone to disturbance in the wild, it is hard for us to hear and therefore study.

Our aim was to: 1) record the elusive boom of the Great Bustard, 2) characterise its acoustic properties, and 3) to describe the behaviour associated with the production of the sound. Here we present the first data on a potentially honest signal of male quality in the highly sexually dimorphic Great Bustard.

Methods

Recording was carried out in April 2011 at the Hawk Conservancy Trust (Andover, UK) using an 8 year old captive male Great Bustard. We used a Marantz PMD671 solid state recorder recording to compact flash at a sampling rate of 44.1 kHz and a Rode NT2-A microphone that has a sensitivity flat range of 20 Hz to 20 kHz. The sounds pressure is described in dB. Measurements were taken between 4:00 and 6:00 p.m. (n = 16 records), under good conditions, with temperatures >15˚C, no wind and no rain. The individual is captive so recordings were made within 2 m and 4 m. The bird was visible while producing all sounds and was in full display for approximately 14 minutes 53 seconds during 5 display bouts. We had 16 separate instances of the drumming sound. The sounds were cleaned and analysed in *Avisoft SASLab*. All recordings were digital and stored on computer. Sound recordings. We measured all sounds at a resolution of 5ms and a frequency resolution of 10 Hz.

As the boom is very low frequency, there was low frequency background noise and simple feedback from the recording device. Therefore, we repeated the analysis on control sample recordings taken during the same recording sessions of the boom.

Results

A boom sound can be characterised as a monosyllabic note of low frequency with a peak frequency energy peak at (mean ± SE) 113 ± 0 Hz (min. 102 ± 0 Hz and max. 129 ± 2 Hz). Although there was background noise at low frequencies, the maximum energy of the boom was different from the background noise of immediately adjacent recordings (Fig. 1). The duration of sound was 0.3 seconds and had at least a 3 second gap between booms (Fig. 2). The sound was emitted only during full gular pouch inflation when only the top of the head was visible. The sound was created during by a small, but notable dip and thrust forward of the head and neck.

Discussion

Here we present the first characterisation of a low frequency sound from a male Great Bustard which is characterised by a specific body movement and a repeatable "note" similar to a percussive drum. We argue that the production of a specific repeatable note is unlikely to be a by-product, but rather a purposefully signal. We cannot agree with the behavioural record of Gewalt (1959) who suggested the sound was emitted during re-inflation but rather it is emitted during a well defined head thrust.

The boom was generally thought unimportant because it was the difficult to hear it and does not travel far (Morales & Martin 2003). Kori bustards and Australian bustards are known to use booms that travel long distance, however, their environment is dominated by bush and semi-desert vegetation which obstruct visual signals. Great Bustard's lek is wide open spaces and can be seen

from several kilometres during displays. When females approach a male they circle the male closely for long periods of time up to 30 minutes (pers. obs.). This is close enough to hear any vocalisation. We argue that once a visual signal has attracted a female to visit the male, he then combines movement and sound production to seduce her.

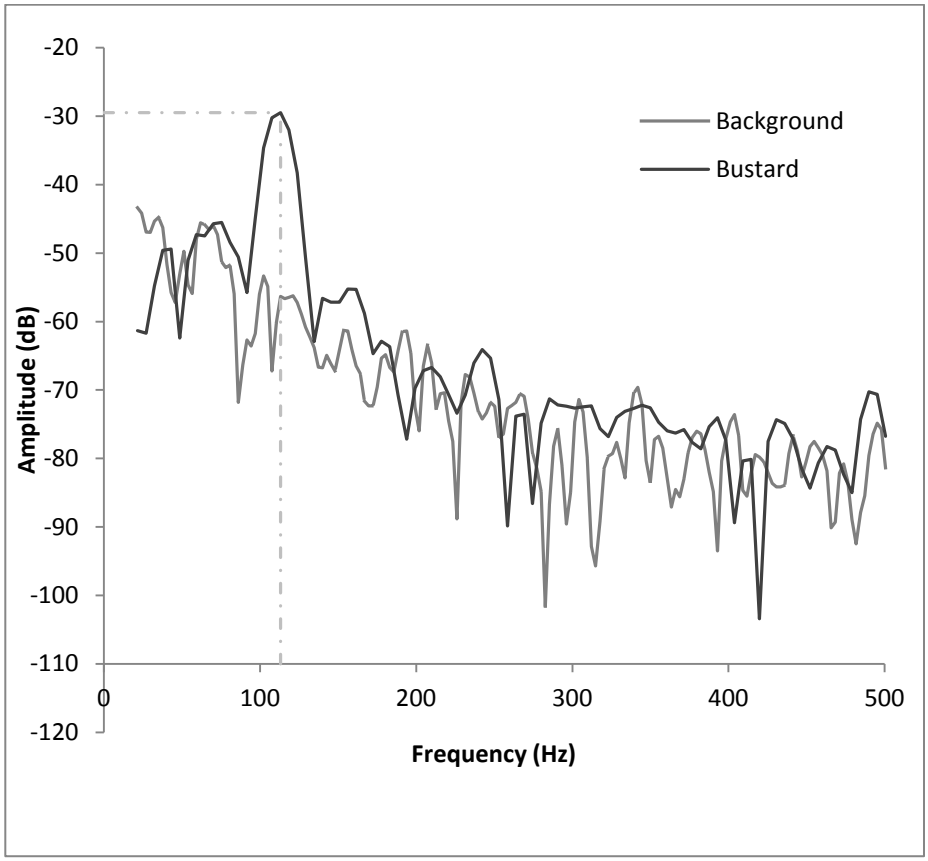

Fig. 1. Frequency spectrum (20 – 500 Hz) for boom made by a displaying 8 year old captive male Great Bustard *Otis tarda*. A reference measurement of background noise taken between display booms. Peak frequency marked with dashed line.

Although we lack samples from other individuals, it is likely that the frequency of a boom would be correlated with the size of a gular pouch, it in itself a highly costly ornament. During the breeding season the gular pouch increases in weight by 1kg due to the infiltration of its connective tissues with fluid (Gewalt 1965). The males inflate their gular pouch, oesophagus and crop during displays which is unique among birds (Gewalt 1965). Furthermore, the crop is not used in digestion (Johnsgard. 1991). The inflated pouch would make a percussive membranous skin and a potential audio amplifier but also holds substantial cost for any male to carry.

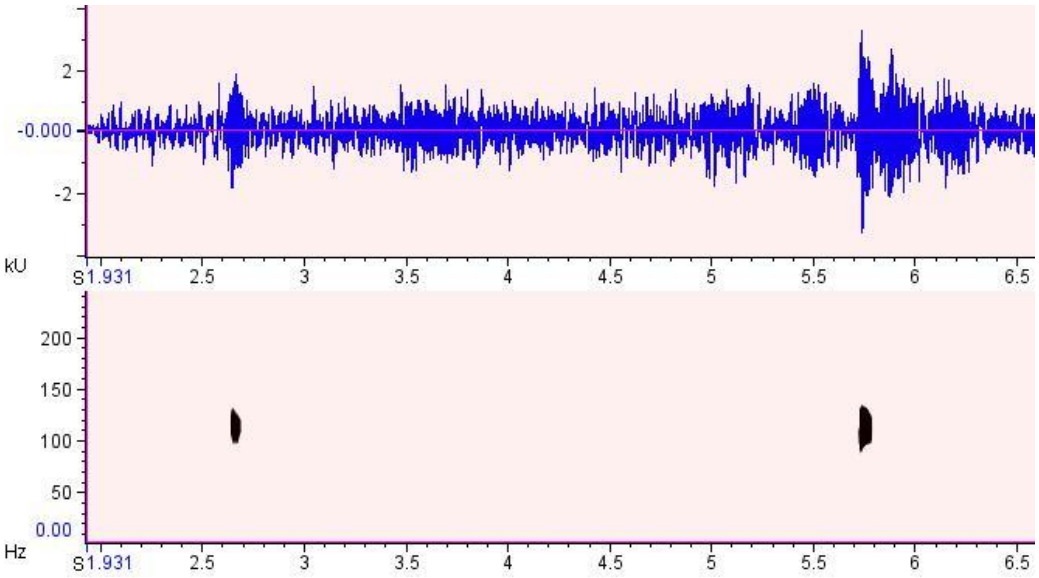

Fig. 2. Wave form (a) and audio spectrogram (b) from a boom made by a displaying 8 year old captive male Great Bustard *Otis tarda*.

Whilst we are unable to establish the exact mechanism of sound production, we hypothesis that the thrusting forward of the head may bang the gular pouch and against the inflated crop. This type of sound is described as mechanical as opposed to syrinx produced sounds as found in song birds. In contrast to many syrinx based vocalisations which are learnt rather than inherited, mechanical sounds are most probably genetically inherited as they are produced my mechanical actions which depend on the phenotype of the individual. Mechanical sounds may be more honest signals of genetic quality than visual displays.

This represents an interesting area for further study for increasing our knowledge of the species and how it evolved such exaggerated secondary sexual characteristics.

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Image 9. This is a Great Bustard conservation awareness poster from the USSR, printed in 1986. It shows bustard friendly farming techniques to improve nesting success. It was given to me by a Russian colleague and this is a scanned copy.

Appendix 2: Great Bustard *Otis tarda* survey results from the Eastern Volga population, Russian Federation, from 2005 - 2009 and 2009 field work report

Robert J. Burnside

Summary

This report provides a summary of data collected from surveys of a Great Bustard population in Saratov, Russia. It builds upon and summarises previous survey results as well as presenting new observational data on display site behaviour.

Introduction

The Great Bustard *Otis tarda* is a globally threatened species that has experienced large-scale range contraction and fragmentation. It is arguably the best known representative of the bustard family (*Otididae*) and has a long documented history in Europe. It is a species that has a complex lek breeding system and extreme sexual size dimorphism.

The Great Bustard is characterised in the literature as a dry grassland/steppe specialist although in some regions it is reported to favour agricultural areas to natural steppe (Gewalt 1959). The steppe holds relatively little avian diversity in comparison to other biomes, but it has several representative specialist species that are also in decline such as the Lesser Kestrel *Falco naumanni*, Sociable Plover *Vanellus gregarius*, Stone Curlew *Burhinus oedicnemus* and Little Bustard *Tetrax tetrax*. Steppe grassland is under pressure from land-use change to agriculture and continuing agricultural intensification. Historically, the Great Bustard is thought to have adapted well to traditional low intensity agricultural practices but now intensification of farming is a threat to the species (IUCN 2012). Other threats to the Great Bustard include power-lines, terrestrial predators, disturbance and hunting (Bankovics 2005; Janss & Ferrer 2000).

Russian population

The Iberian population of Great Bustards is substantially larger than any other existing population containing about 60% of the world population (Palacin & Alonso 2008). It is currently considered genetically isolated from the central and eastern European populations (Pitra et al. 2000) and thus sub-populations need to be considered as independent conservation units. Russia is thought to contain about 20% of the world populations and 70% of the central and Eastern European population (Oparin et al. 2003; Watzke et al. 2007). This is the most important population and represents the best conservation prospect for the Great Bustard in Eastern Europe.

The Great Bustards' range within Russia has contracted over the past 50 years (Oparin et al. 2003). Consequently, in Russia, is it classified as a Red Data Book Species and is legally protected against hunting. Within Russia, the Saratovskaya Oblast (Saratov) is the most important area for Great Bustards, containing the largest concentration of Great Bustards in Russia. It is thought to hold between 8,000 – 10,000 individuals and is also thought to be stable (Oparin et al. 2003). However, with continued economic growth and increasing agricultural intensification the populations have become increasingly threatened and continued monitoring of the population is important. Thus, I had objectives several objectives:

Objectives

- Carry out spring survey
- To identify and map the breeding areas in Saratov region.
- To observe Great Bustard mating behaviour.
- To collect data on nesting locations
- Collate and digitise previous surveys and breeding data

Methods

Study region

The Saratovskaya Oblast (Latitude 50.70, Longitude 46.99) is an administrative region in European Russia that lies on the border of Kazakhstan and represents the western edge of the Eurasian steppe biome. It is approximately 100,000 km^2 and divided by the River Volga. Agriculture is the

predominant industry, accounting for 43.2 % of land-use at the end of the 20th century. Virgin land accounts for 19.6 %, fallow for 8.9 %, unused land for 18% and settlements, waterbodies, roads and forests account for 10.3 % of land cover (Oparin et al. 2003; Watzke et al. 2007).

The study area is located on the east side of the Volga which has a drier climate and less tree cover than the western side. The study area covered a 7600 km^2 area that is divided into 20 km by 20 km grids (Fig. 1). This is the existing sampling units used by the Severtsov Institute and it was appropriate to follow similar methods for comparability

Spring survey

Spring surveys were carried out in 2008 and 2009. A survey area of 19 adjacent 20km x 20km squares (Fig. 2) were surveyed between 10th April and the 20th April. Four teams of two observers covered the 400km^2 areas in a 4x4 vehicle. The routes were not pre-determined and are often limited by the availability of dirt roads, changes in seasonal water bodies and precipitation. Vehicles were intermittently stopped at vantage points to scan the landscape with a telescope and binoculars. All Great Bustards sightings were recorded either with GPS (estimating distance and bearing to the centre of the group) or on a 1:100,000 scale map and later digitised to WGS1984 datum and projected in UTM WGS1984 38N. At each sighting, the number of individuals, sex (where identifiable), habitat and behaviour were recorded. The 2008 survey had the same methodology but covered less area than in 2009 due to extreme weather conditions limiting movement.

Autumn surveys

Autumn surveys were carried out in 2005, 2006, 2007 and 2008. Autumn surveys were carried out with the same technique as described above. However, different extents were covered each year and at different times (Table 1). The previous survey results were digitised in WGS1984 datum and projected in UTM WGS1984 38N.

Table 1. Dates of Great Bustard surveys in Saratov from 2005- 2009

Year	Season	Survey dates
2005	autumn	Not recorded
2006	autumn	19th-26th September & 9th-10th September
2007	autumn	15th-18th October
2008	autumn	29th September -5th October
2008	spring	11th-16th April
2009	spring	10th -18th April

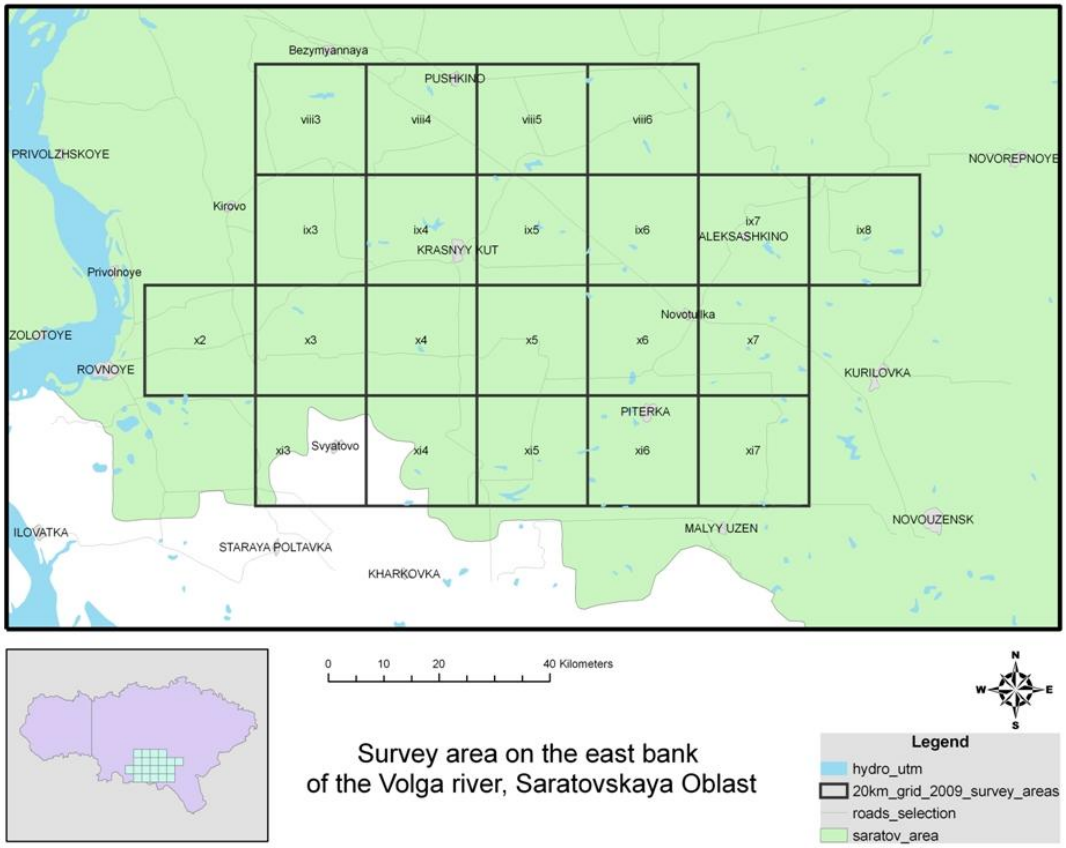


Figure 1. Survey area covered in Spring 2009, divided into 20 km x 20 km quadrants.

Nesting in 2009

It is very difficult to locate Great Bustard nests using traditional searching techniques in Saratov due to the size of the fields and extent of the area. However, due to the continued practice of egg rescue from nests under threat of destruction from agriculture, tractor drivers inform the Severtsov Institute field station of Great Bustard nests during cultivation. The sample is, however, biased because the main activity of farmers at this time is tilling and cultivating the land and therefore is not representative of all potential nesting habitats.

Nests locations were recorded using GPS. The number of eggs, presence of other species and storage method were also recorded. Width, breadth and weight of eggs was measured at the field station using callipers. Results from 2006-2008 egg collection seasons were also digitised when possible. Lay date was calculated as being 28 days before the hatch date. For every chick that hatched I recorded the weight (g), tarsus length (mm) and head-bill (mm).

Lek behaviour

Four different leks were visited to monitor display behaviour of male great bustasrds in: Talovka, Borisoglebovka, Alecsashkino and Vologrd region (outside the administrative district of Saratov). A hide was positioned in tree lines with a view of display area. From the hide, the behaviour of Great Bustards was recorded. Time, temperature, location, number of males, number of females present and a video record was made where possible for future analysis of display longevity. The

leks were observed mainly in the morning for logistical reasons although efforts were made to distribute effort as evenly as possible.

Analysis

The distributions within the study area, extent 7600km^2, were tested for spatial randomness with a nearest neighbour analysis. The results of autumn surveys were pooled for this analysis.

Ecogeographical and anthropogenic variables

I calculated straight-line distance from Great Bustard observations or roads and settlements. These were each calculated on a raster layer with a 100m x 100m resolution. Elevation data was downloaded from the United States Geographical Service's Shuttle Radar Topography Mission dataset and sampled at 100m resolution. The mean value for the predictors within the 1km x 1km grid was calculated with Arc Spatial Analyst Zonal Statistics. Each zonal grid square took a value of 1 or 0 to denote presence and absence respectively. An equivalent number of grid squares with absences were selected at random quantify the difference in presence and random sites.

Results

Autumn survey 2005-2008

The total number of birds counted during the survey fluctuated between years with no notable trend (Table 2). The median flock size of 5 individuals but ranged from 1 to 75 individuals (Fig. 2). Flocks were composed of 41% male, 21% female, 13% juvenile and 24% unidentified. These estimates were consistent between years except in 2007 which saw a high proportion of females (Fig. 3). The juvenile recruitment/productivity to autumn is consistently estimated between 10 and 20%.

The density of birds per kilometre was never greater than 0.1 birds/km^2 (Table 2). From the combined data, locations were spatially clustered showing a significant difference from a random distribution (Expected Mean Distance = 3323m, Observed Mean Distance = 2459m, Z Score = -6.52, $p<0.05$). Although sightings were clustered, the areas utilises during the pre-migration flocking seem evenly distributed over the study area (Fig. 4).

Table 2. The results of autumn surveys for Great Bustards in Saratov from 2005-2008.

Quadrat Code	autumn 2005		autumn 2006		autumn 2007		autumn 2008	
	Individuals	Flocks	Individuals	Flocks	Individuals	Flocks	Individuals	Flocks
VIII3	17	1					0	0
VIII4	51	2	46	4			8	1
VIII5	24	2	0	1			17	1
VIII6	61	12	5	3	0	0	1	1
VIII7	9	3	3	2				
IX2			6	3				
IX3	23	5	0	1			43	4
IX4	2	2	0	1	0	0		
IX5	45	5	39	3	0	0	0	0
IX6	119	12	96	6	73	4	35	2
IX7			8	4	25	2	35	3
IX8							0	0
X3			6	1	0	0	12	3
X4	35	2	34	6	0	0	33	2
X5	22	1	61	4	38	1	4	1
X6	0	0	3	1	17	1	51	4
X7	194	7	64	7				
xi2							0	0
xi3								
xi4	0	0			0	0	14	2
xi5	8	1	43	9			103	3
xi6			22	4				
xi7			7	5			81	3
Total	610	55	443	65	153	8	437	30
Median/Q	23	2	7.5	3	0	0	14	2
Total quadrats surveyed	15		19		10		17	
Total area Surveyed (km2)	6000		7600		4000		6800	

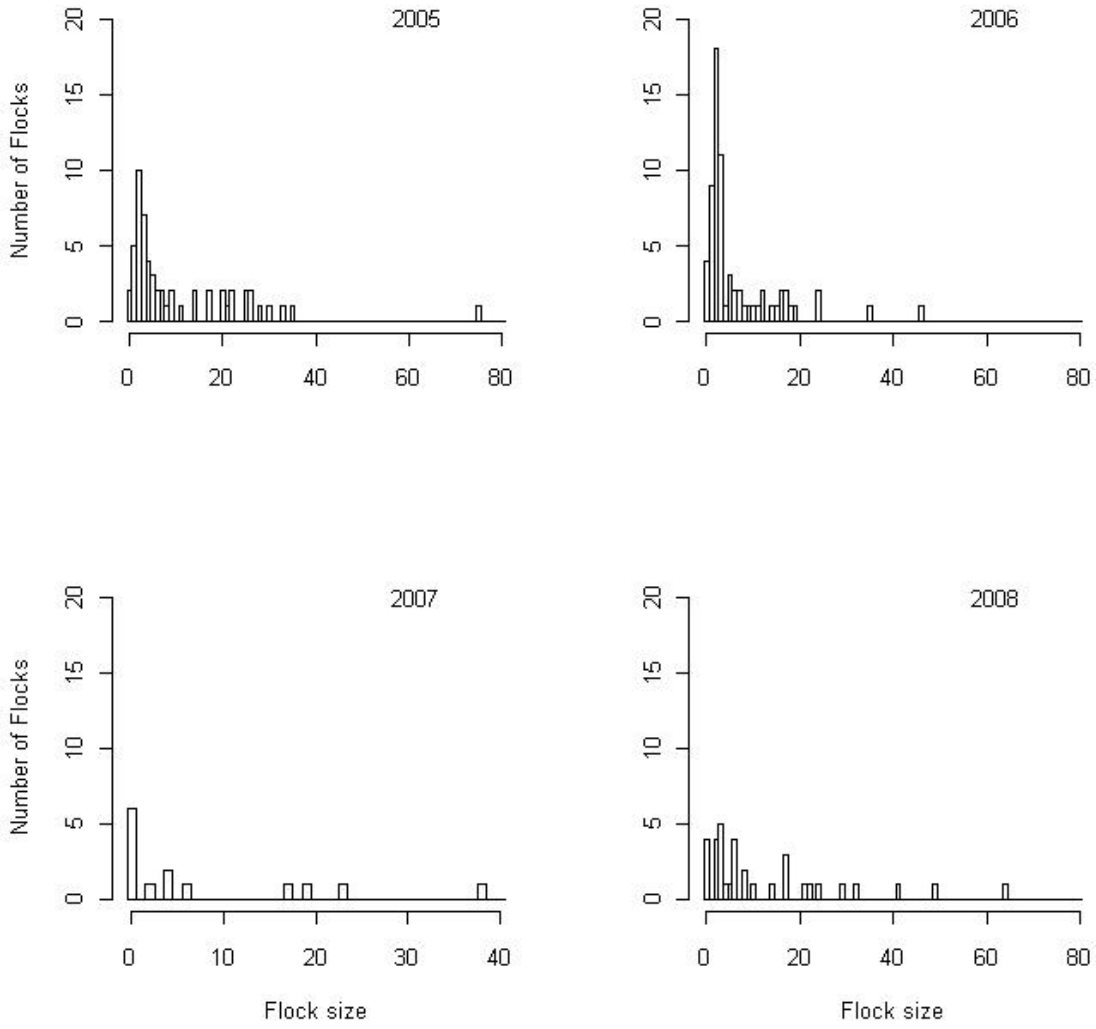


Figure 2. Frequency histograms of Great Bustard flock sizes during autumn surveys from 2005-2008. Flock size of 0 represents the number of quadrats that had absences.

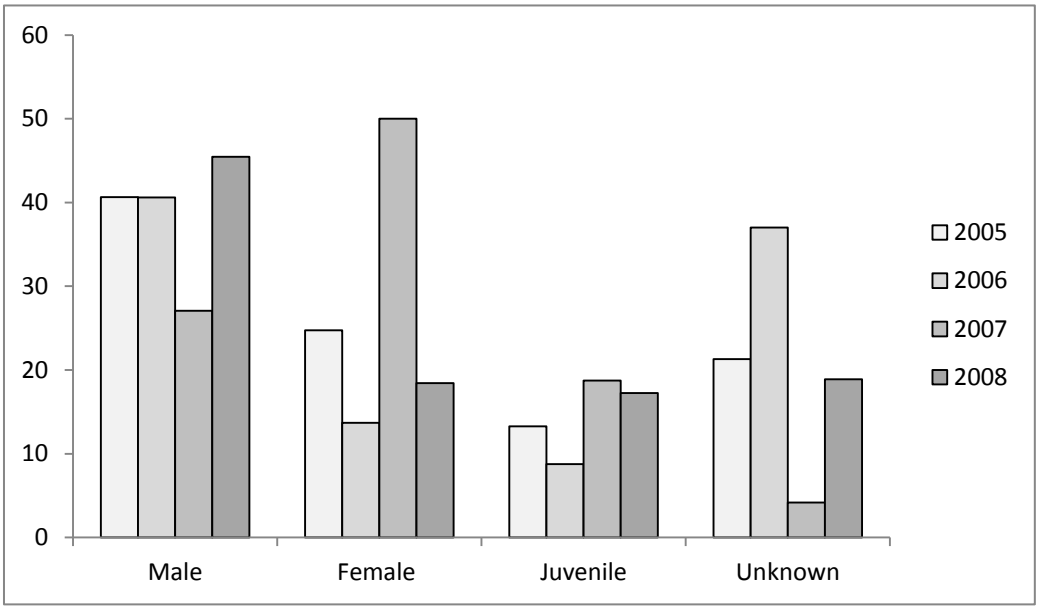
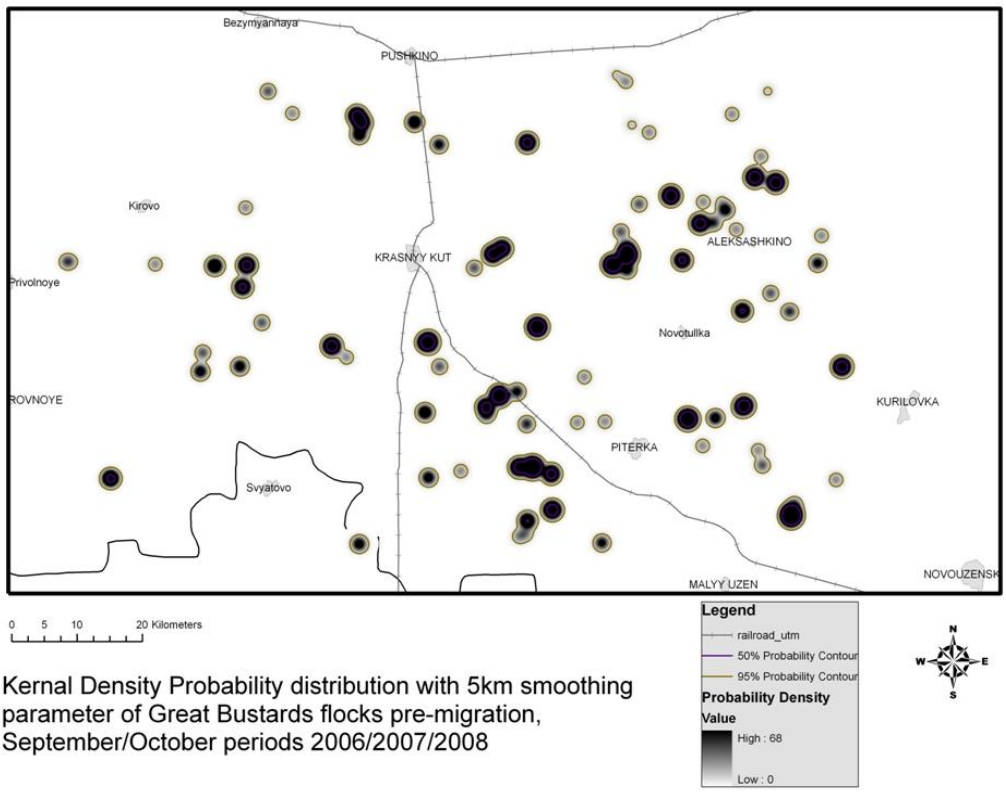


Figure 3. The proportions of each sex observed during autumn surveys of Great Bustards in Saratov from 2005 - 2008.

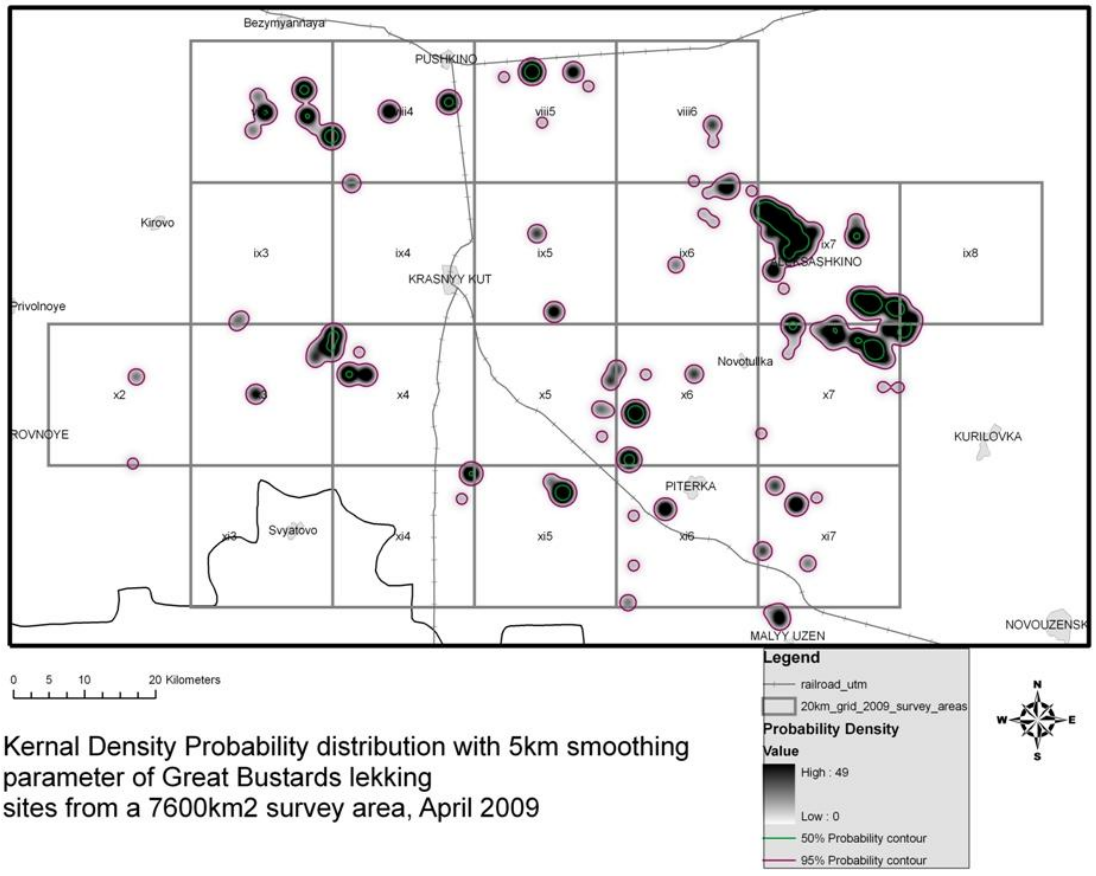


Kernal Density Probability distribution with 5km smoothing parameter of Great Bustards flocks pre-migration, September/October periods 2006/2007/2008

Figure 4.

Spring survey 2009

A total of 693 individuals were recorded (Table 3), while median flock size was 5 individuals with a range of 1 – 32 individuals (Fig. 6). Locations of Great Bustards were clustered over the 7600km^2 survey area (Observed Mean Distance = 2029m, Expected Mean Distance = 3403m, Z-score = -9.9, p = 0.01). The areas utilised at the beginning of the display season had the highest concentration east of Krasnyy Kut (Fig. 5). The demographic composition of the overall survey was similar to that found in spring, 21 % unknown, 29 % female, 50 % male, with the exception that no juveniles are identified. Great Bustards were observed farther from roads and settlements than you find from a random selection of absence sites (Table 4).



Kernal Density Probability distribution with 5km smoothing parameter of Great Bustards lekking sites from a 7600km2 survey area, April 2009

Figure 5.

Table 3. The results of spring surveys for Great Bustard in Saratov from 2008 and 2009.

Quadrate Code	Spring 2008		spring 2009	
	Individuals	Flocks	Individuals	Flocks
viii3	31	7	55	7
viii4	19	2	19	2
viii5			32	5
viii6			2	2
ix3	19	3	3	3
ix4	15	2	3	1
ix5	13	3	8	2
ix6	98	16	226	34
ix7				
ix8			88	32
x2			3	2
x3			52	13
x4			0	0
x5			10	5
x6			47	5
x7			73	20
xi4			10	2
xi5			27	2
xi6			22	6
xi7			13	5
Total	195	33	693	148
Median	19	3	19	5
Total quadrates surveyed	6		18	
Total area Surveyed (km2)	2400		7200	

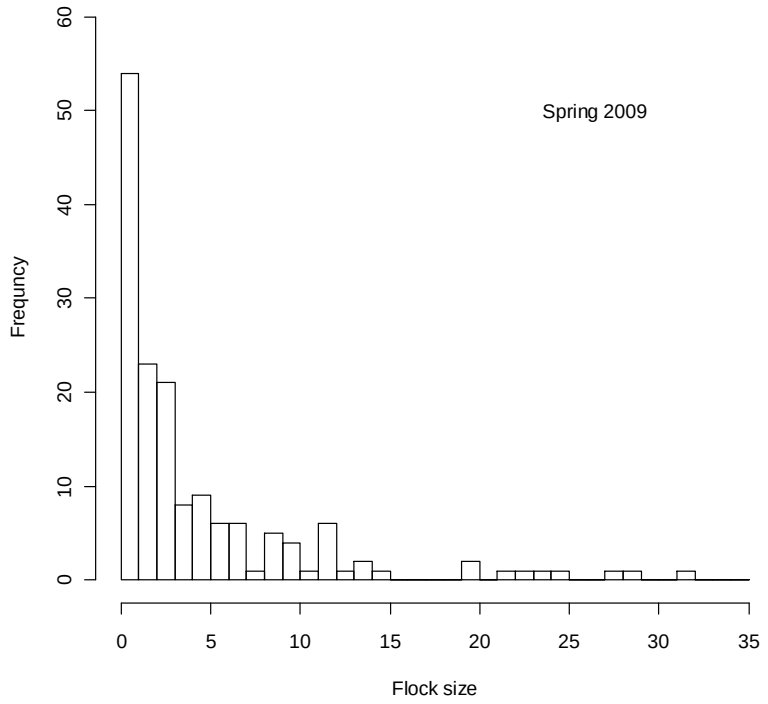


Figure 6. Great Bustard flock sizes from spring survey 2009.

Table 4. Mean variable values for Great Bustard presence and absence sites

Variable	Great Bustard sites			Random absence sites		
	Mean	±SD	N	Mean	±SD	N
Distance from roads (m)	4842	3039	131	3894	2932	131
Distance from towns (m)	8460	3889	131	7246	4144	131
Elevation (m)	70	11	131	64	15	131

Nesting

From 2006 to 2009, 96 nests were reported (Table 5). The majority of the nests were found in the Fedovskaya region (Table 6). Mapping the locations of nests from 2009 indicates hotspots around Alecsashkino village on the boundaries of the largest lek (Fig. 8).

The mean clutch size was 1.89 eggs per nest and egg morphometrics are presented in Table 7. Under incubation protocol outlined by Pereverzina and Waters (2008), there was 79% hatch rate. Chick morphometrics are presented in Table 8.

Table 5. Number of nests found between 2006 -2009

Year	Number of nests
2006	19
2007	20
2008	29
2009	28
Total	**96**

Table 6. Regional numbers of Great Bustard nests found between 2005 and 2009

Region	Engelsky	Federovsky	Krasnyykusky	Pietersky	Sovyetskee	Not reported	N
Number of Nests	3	57	8	23	1	3	96

Table 7. Morphometrics of Great Bustard eggs and clutch size.

	Mean	±SD	n
Clutch size	1.89	0.65	96
Weight(g)	135.9	11.77	152
Length(mm)	79.16	3.83	152
Width(mm)	56.75	1.85	152

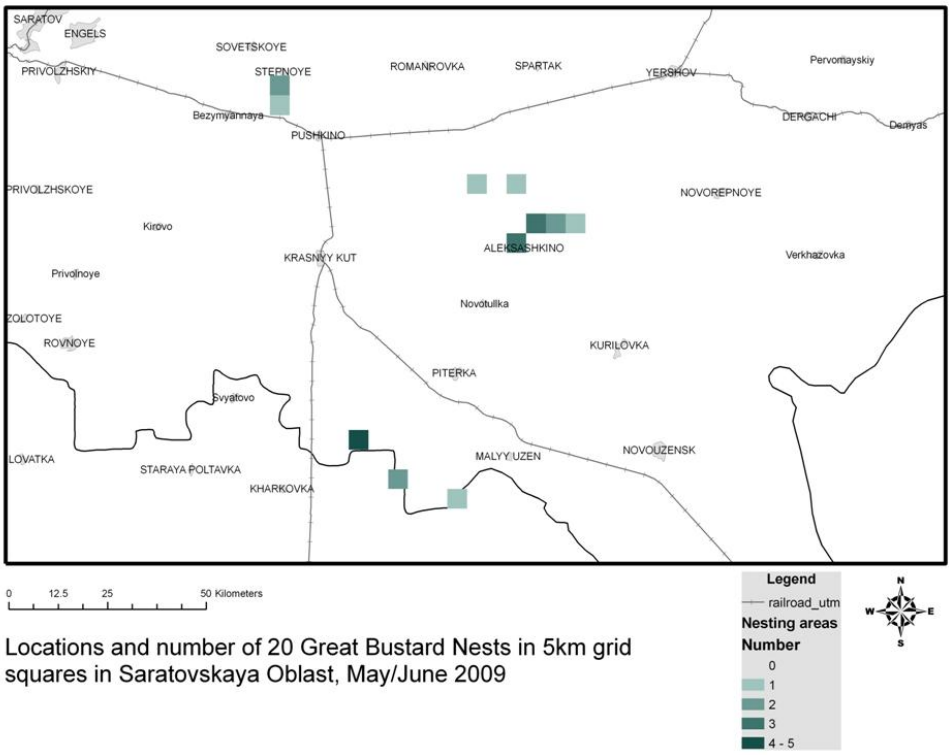


Figure 8. The locations of Great Bustard nests, 2009.

Table 8. Morphometrics of Great Bustard chicks hatched in spring 2009.

	Mean	±SD
Bill length (mm)	23.99	1.33
Bill width (mm)	12.73	1.04
Tarsus (mm)	37.14	1.15
Middle toe (mm)	12.35	1.42

Breeding behaviour

The first display was witnessed on the 14th April 2009 and the last witnessed on the 24th May 2009. The display period lasted approximately two months with some sporadic displays outside of this period. By June, the numbers of birds found at the lek sites had decreased. In 60 hours of lek observation, I witnessed around 200 displays, mostly with females present. However, only one copulation was recorded during this time.

The frequency of display from dawn to dusk had a bimodal distribution and the displays were performed most between 10-15°C (Fig. 9). The dates of predicted laying for the first and last

clutches reported were consistent between years, the first clutches being laid in the 3rd decade of April and the last in the first decade of June (Table 9).

Table 9. Predicted lay dates of Great Bustard clutches in Russia.

Year	First lay date	Last lay date
2006	24th April	3rd June
2007	28th April	10th June
2008	18th April	4th June
2009	26th April	3rd June

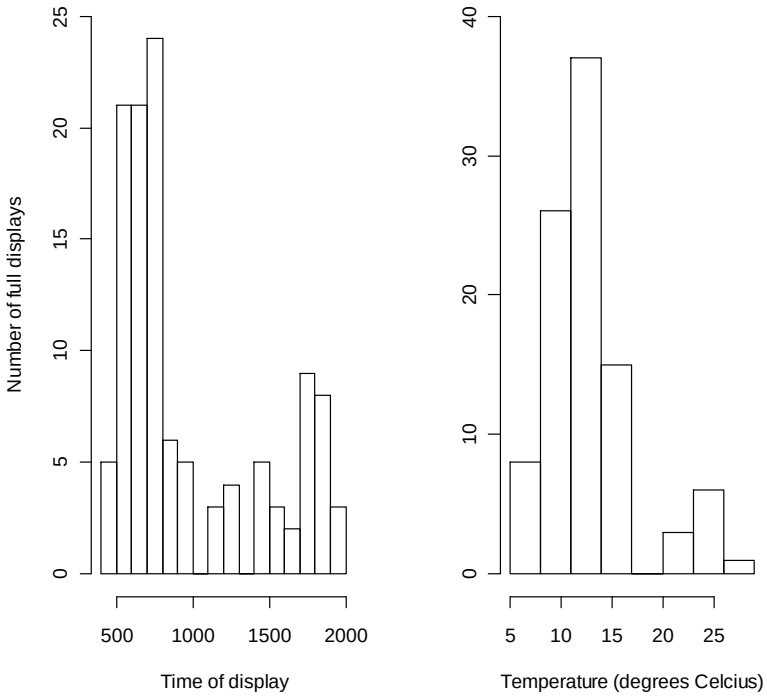


Figure 9. Histograms of the number of Great Bustard males observed displaying at different times of the day and at different temperatures.

Discussion

Autumn surveys

This report summarises the range of descriptive data collected during five years of population surveys and during the 2009 field season.

The last published population estimate for Saratov population was in 2003 (Oparin et al. 2003) from a three year project completed in 2000. The results presented here are from comparable surveys carried out from 2005-2009. However, there are inconsistencies in the timing and spatial locations of the autumn surveys resulting in different efforts between years. For example, the 2007 autumn survey was in mid-October; most likely after the migration would have begun and explains why the numbers were low numbers in that year and less squares were surveyed. Consequently, it is difficult to confidently assess trends from these survey data. However, the counts in 2005, 2006 and 2008 are comparable.

It would be misleading to estimate the total population in all of Saratov by extrapolation from this data without full habitat availability analysis. Further, bird distributions showed significant clustering which invalidates the use of extrapolation because birds would be distributed unevenly. Even so, for comparison we see these surveys have a comparable density estimates of 0.1 birds per km^2 to those found by Oparin et al. (2003).

The autumn surveys can help identify productivity in the population because juveniles can be identified within the flocks. In all autumn surveys, consistently 10-20% of individuals were categorised as juveniles which is equivalent to productivities of 0.04 to 0.29 seen in Iberian populations (Martinez 2008; Morales et al. 2002).

Spring surveys

The most comprehensive spring survey was conducted in early April 2009. Four exploded leks were observed in the 7200km^2 study region. There were differences in the total number of males observed at the leks ranging from 14 to 100 males at the largest lek. More birds were counted during 2009 than in previous years. This could be due to increased effort or rather timing the surveys when migratory flocks arrive and before females disperse for nesting.

Leks arenas are highly traditional and new leks are rarely formed (Alonso et al. 2004). I noted two previously known display areas which had become extinct in recent years. One independent exploded lek in the Lepinhenka area and one lekking patch within the Borisoglebovka exploded lek. Both areas had recently been abandoned by the owners, allowing the areas to become inundated with fallow weeds. The structure of this tall vegetation seems to reduce habitat quality for Great Bustards.

Breeding behaviour

Breeding phenology was comparable in timing and length to previous estimates in Saratov (Watzke 2007). The first estimated hatch dates were 10 days after the first displays were observed. After which the peak period for nest reporting was May and early June. The main disturbance to the population of Great Bustards in this region is farming practices, such as tilling, sowing and harvesting, which coincide with nesting and the critical period of pre-fledging when chicks are flightless.

Male Great Bustard display patterns were influenced by time of day and temperature in a similar way to birds in Iberia (Detrucios & Carranza 1991). The display period had finished by early June and attempts were made to survey for mother and chicks. However, no chicks were recorded in five days of survey in June. The surveys were too early to enable observation of chicks as they are shy at this point and the females remain solitary.

Between 20 and 30 nests were consistently found each year from 2006 - 2009. The sample indicates that the nesting rates in this area have remained stable, assuming farmers report nests consistently between years. Nests were mainly found in tilled fields. However, these samples may be misleading for use in estimating nesting habitat preference because few other habitats were sampled with the same intensity. A similar bias in nest reporting rates may also be found between regions. The Federovsky region accounts for 60% of all nests found over the four years and Pietersky for 35%. Federovsky has the largest population of birds identified during surveys and also seems to be an important nesting area (Fig 10). Currently, it holds the only designated conservation area in the region, close to the town of Borisoglebovka, and was designated as official reserve since approximately 1981 (Krustov. pers. comm. Fig 10). The conservation zone currently captures portions of the highest density lek and nesting areas (Fig. 10). It is unclear if other areas hold productive nesting areas as there are varying levels of communications with farmers in different regions.

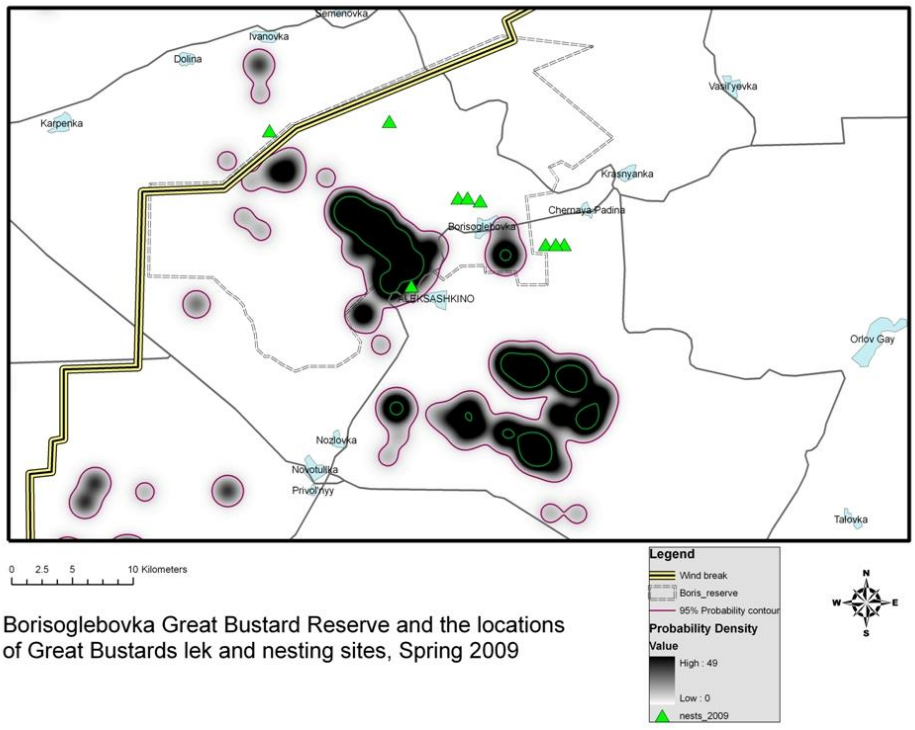


Figure 10. Map of the Borisoglebovka Great Bustard protected area and the location of displaying birds and nests from 2009.

The vast majority of the survey area is agricultural and consequently all observations of Great Bustards were on crops, mainly young wheat. However, preliminary results showed that Great Bustard presences were farther from roads whereas towns had less difference. Great Bustards in this region are very wary of cars and often flush at large distances of a 1-2 Km's when a vehicle

approaches. This may be caused by a legacy of hunting from cars. On the other hand, Great Bustards are also known to be affected by disturbance from roads (Chapter 5, this volume). In the future it may be worth creating different levels of settlements to capture the variation in industrial areas and farming towns. The two largest leks at Borisoglebovka and Alecsashkino are closer to their respective villages than other leks in the study area.

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Appendix 3: A review of recent research the Great Bustard (*Otis tarda*) ecology and conservation

Robert John Burnside

Completed March 2009

Background

Studies on Great Bustards have not been limited, as there is a fair variety of published articles and a quick search for *Otis tarda* on ISI Web of Science returns approximately 60 articles (10 March 2009). This represents the majority of English language research publications published in peer-reviewed journals. But there is a wealth of literature from across Europe, Spain and the East that is often difficult to access due to publication in foreign languages. However, until recently, studies were often limited to observational descriptions, concentrating on habitat use, foraging and censuses with no long term studies of marked populations. There are notable difficulties in studying Great Bustards, such as the scale of study due to size of the steppe habitat it utilises and they are extremely shy of humans. It has recently become possible with advances in GPS and satellite technology to study broad scale patterns in its ecology and distribution. This has produced some notable studies from the Iberian population looking at regional and landscape scale habitat utilisation. Also, studies on genetic diversity, population relatedness and gene flow have revealed interesting findings about the movement of birds. These methods have also been complemented by behavioural studies on marked populations of birds in Iberian. The vast majority of reputable studies come from the Iberian population.

Population status

It is appropriate to start this discussion with an overview of the current global status of Great Bustards. Historically, the Great Bustard has experienced massive declines in population size and range, in both its breeding and non-breeding range (Morales & Martin 2002). Some national populations have experienced dramatic population reductions such as in Germany with a collapse from 4000 to 50 birds within the span of 50 years (Langgemach 2008). A similar story can be told for the Hungarian population which decreased from approximately 3,400 in 1980 (Collar 1985) to 1,100 in 1996 (Farago 1996). Range reductions have also been reported in Russia (Bustard Studies 2), Spain (Alonso et al. 2005a) and Portugal (Pinto et al. 2005) by the loss of leks over the past three decades. There are notable historical national extinctions (UK, France, Italy and Greece), recent national extinctions (Yugoslavia and Poland) and populations that have been reduced to such small sizes that there will be no return if drastic intervention is not taken (Romania, Czech Republic and Slovakia) (Palacin & Alonso 2008). These declines warranted the Great Bustard to be classed as vulnerable in the IUCN red list since 1994 and further decreases are predicted with future land-use change in Europe (IUCN, 2008).

The current world population estimate is 43,514 - 51,227 individuals (Table 1) (Palacin & Alonso 2008). The authors highlight quality issues with some of the available census estimates. Even for the world's heaviest flying bird, the scale of the logistics needed to census populations has hindered accurate estimates. For example, since 1994 the species has been classified as vulnerable (IUCN, 2008) with a decreasing population trend, but since 1991 the global population estimates have grown from 28,000 (Collar 1991) to 31,000-37,000 in 2000-2007 (Birdlife international 2000), until now with a current estimate of 43,514 - 51,227 (Palacin & Alonso 2008). This increase in world population estimate is probably attributable to the change in Iberian population estimates alone. Within Spain (arguably the best studied population), population estimates have been largely underestimated, increasing from 17,000 in 1996 using extrapolation (Alonso & Alonso 1996), to 24,490 in 2003 (Alonso et al. 2003) to 27,000-30,000 in 2007 (Palacin 2007).

The degree of inaccuracy of population estimates over the past two decades has highlighted the need for appropriate census techniques for the Great Bustard. Trends in population dynamics are probably more important than absolute population numbers to an extent. However, accurate census figures are needed to quantify the status of a population. Even though global population estimates have been increasing there have been notable extinctions of leks throughout the range (Alonso et al. 2003) and increasing habitat fragmentation (Martinez 2008). One common conclusion from all authors was how fragmented populations were and the proximity of threats.

Habitat

Great Bustards experienced a range expansion during the 18th century with the proliferation of agriculture and deforestation throughout Europe and Russia. It adapted well to the low intensity agriculture practiced during these time and shifted from natural steppe grassland to cereal agro steppe (Gewalt 1959; Morales & Martin 2002). This adaptation was so beneficial that the species now shows a preference for agricultural land over natural steppe (Lane et al. 2001; Martinez 2008; Osborne et al. 2001). However, modern farming methods and intensification are noted for causing bird declines and habitat loss.

The Great Bustard shows different habitat preferences throughout its yearly behavioural cycle of breeding, post-breeding and migration and between the sexes (Moreira et al. 2004). On a local scale, Great Bustards prefer flat dry grasslands found on chalk and limestone, or well drained soils with few trees (Gewalt 1959; Lane et al. 2001; Osborne et al. 2001). However, different regional populations

have shown different habitat preferences. Portuguese bustards have been shown to have a habitat preference for stream margins (Moreira et al. 2004) and this has been noted once in Caceres in Spain (Moreira et al. 2004). It has been also been noted in eastern Russian population as well as their tendency to utilise habitat near trees whereas they are noted for avoiding streams in other populations.

In considering the habitat preferences of Great Bustards, it is appropriate to think of habitat avoidance. Great Bustards avoid forested areas, and afforestation is noted as a cause of lek extinctions in Portugal (Pinto et al. 2005). Farming regimes that decrease the amount of fallow, cereal and legume fields, and an increase in the proportion of permanent pastures, fodder, irrigated crops and livestock densities have been noted to negatively affect bustard presence (Alonso et al. 2004; Lane et al. 2001; Martinez 2008; Osborne et al. 2001). The proximity of roads, tracks, villages, irrigation, buildings, villages, railways, rivers, fences and power lines cause decrease in lek density by increasing disturbance (Pinto et al. 2005). Similar patterns have been indicated Russia (Oparin et al. 2003; Watzke et al. 2007) and Hungary (Bankovics 2005) .All these factors can be taken into account in the quantification of habitat utilisation and availability and for example, although food levels, substrate type, and topography may remain unchanged, the presence of new disturbances may decrease the quality of the habitat causing reduction in available range.

The analysis of landscape scale patterns of habitat availability in Spain, quantified in terms of Great Bustard preferences and avoidances, have shown some interesting results on Great Bustard habitat utilisation. Available habitat that is identical to existing Great Bustard habitat remains unutilised or not colonised (Alonso et al. 2004; Lane et al. 2001; Martinez 2008; Osborne et al. 2001). Classically, it is thought that individuals sample habitats to determine its quality but in these studies, habitat quality was indistinguishable between the measured variables. There is always the possibility of an invisible factor, such as illegal hunting or pesticides, but the authors suggest these are homogenous in the region. Even more compelling is the fact that from over 20 years of surveys in Spain and Portugal, no new leks have been recorded (Alonso et al. 2004; Pinto et al. 2005). Great Bustard's have a low ability to colonise new areas and high natal philopatry in females. On the other hand, when populations are declining, they are unlikely to expand and colonise new areas. But with notable extinction of leks, birds that were displaced from the low quality habitat probably moved to "higher quality areas". Instead of utilising available empty habitat it appears the birds have chosen to settle at existing leks. This is indicated by the rate of population growth at some leks which is higher than capable through natural reproduction alone (Alonso et al. 2004).

Two possible hypothesises could explain the pattern discussed above, but realistically it will be a mixture of both. The bustards may be using conspecifics as an indicator of habitat quality rather than

sampling habitat themselves (Alonso et al. 2004), or they are a social bird that prefers to be in the presence of its conspecifics for reasons of sociality, reduced risk to predation and increased mating opportunities.

Martinez (2008) found that on a regional level, leks with higher density had a lower productivity than other leks. A potential explanation for this is that mothers and chicks need a large area over which to forage and high density would lead to density dependent reduction in productivity. Concentration of individuals at higher quality sites may have other potentially deleterious effects.

There are two very important implications for population management in these results. One that even if one restores habitat from where Great Bustards are absent, or extirpated, simply making the habitat available may not lead to colonisation or the creation of a new lek. Therefore it is important to maintain existing leks. Secondly, using the presence of conspecifics in areas that you want colonised may potentially be possible, by imprinting a bird onto a new area and thereby increasing the chance that individuals undertaking natal dispersal may recruit into this new group or site.

As well as inhabiting different foraging areas throughout the year, bustards can either inhabit these areas at a low density or in a highly congregated fashion, during post-breeding and pre-breeding activity. Bustards inhabit the landscape at a very low density in of approximately 1 to 2 birds per km^2. Though useful for comparison, this measure does not reflect the behaviour of the bustard throughout the year, where it often is highly aggregation.

Reinforcing the case for the conspecific attraction are studies from Portugal and Spain, showing that large populations of bustards are growing, whereas small populations of bustards are getting smaller (Alonso et al. 2004; Pinto et al. 2005). The evidence in Spain is convincing in its support of conspecific attraction as the habitats between leks is homogenous in substrate, crop regimes and disturbance. There is no significant relationship between population number and habitat quality. Large leks are also increasing at a rate beyond their capable productivity output suggesting immigration from other areas. Pinto et al. (2005) suggested that habitat degradation is the cause of emigration. Degradation of habitat at leks can potentially cause emigration, to higher quality areas but leads to a reduced ability of a population to cope with stochastic events if they are concentrated in few areas. Small populations in Portugal were under pressure from disturbance and habitat change. Many movements of individuals have been to high quality habitat nature reserves which now holds approximately 90% of Portugal's population (Pinto et al. 2005).

To further understand habitat utilisation, population dynamics and colonisation potential we need to quantify the Great Bustard's dispersal.

Country	Number of. birds (min-max)	Reference	Quality of estimate
Spain	27,500 - 30,000	Palacín, 2007 (updated); Junta de Castilla y León, 2008	high
European Russia	8,000 - 11,000	Malikov *et al.*, 2000; Khrustov *et al.*, 2003; Antonchikov, 2006; Watzke *et al.* 2007	medium
NW China (Xinjiang)	2,000 - 3,000	Gao *et al.*, 2007	low
Mongolia + SE Rusia +NE China	1,500 - 1,700	Goroshko *et al.*, 2004	high
Portugal	1,399	Pinto and Rocha, 2006	high
Hungary	1,353	Túzokvédelmi Program, 2006	high
Turkey	764 - 1,250	Kiliç and Eken, 2004	low
Ukraine	500 -850	Domashlinets and Andriushchenko, 2004; Yaremchenko and Bakhtiyarov, 2006	low
Austria	175	Raab, R. *pers. com.*	high
Iran	89 - 161*	Amini, 2000	low
Germany	110	Langgemach, T. pers. com	high
Morocco	91 - 108	Alonso *et al.*, 2005b	medium
Kazakhstan	0 - 50	Academy of Sciences, 1996	low
Serbia and Montenegro	35 - 40	Garovnikov, 2004	high
Slovakia	8 - 16	BirdLife International, 2004b	high
Czech Republic	1 - 6	Škorpíková and Horal, 2004	high
Romania	0 - 4	Istvan Leszai, *pers. com.*	high
Moldova	0	BirdLife International, 2004b	high
Bulgaria	0	Deleriev *et al.*, 2004	high
TOTAL	43,514 - 51,227		

* this maximum corresponds to an autumn count in 1991.

Table 1. Current estimate of Great Bustard breeding populations, ordered by numbers of birds. Taken from (Palacin & Alonso 2008).

Life History (Table 2)

Dispersal

Dispersing between groups, individuals transfer genes, affect the abundance of a species at a site, colonise new sites and affect the dynamics of sub-populations. This is especially true in meta-populations where the immigration and emigration can have strong effects on the persistence of a population. Due to the lack of long-term marked studies on bustards throughout their life-time, there is very little information on how Great Bustards move around throughout their life. However, there is some good information on the natal dispersal (movement from the natal area to the area of first breeding) of Great Bustards, this is partially because there is a reasonable chance of following Great Bustards for the first few years with radio transmitters and it is easiest to catch the chicks. Radio-tracking devices are often preferred because of their long-life, however there is a lot man hours needed to track Great Bustards which can travel up to 180 km or farther during their natal dispersal which means a large number of birds are lost. Satellite transmitters are the preferred form of tracking as they can give fine scale resolution on movements and large scale movements on migratory patterns. Understanding these life history traits is important when designing conservation strategies.

In Russia, for example, the use of radio transmitters has been unsuccessful due the size of the area that the birds use, meaning there is an extremely low chance of finding the birds (Khrustov, pers comm.). Germany has successfully used transmitters in their supplementation project, but the transmitters they use provide only short-term data, meaning they have good information on the first few months/years, and very little on the birds that make it through the perilous first few years of life (Eisenberg 2008).

Monitoring has many different methods, outlined by Alonso (2008). The use of wing tags is very important but ultimately it is hard to identify birds when you cannot find them. Alonso (2008) describes the use of radio-transmitters as “essential” for any reliable study into the life history of the Great Bustard.

Table 2. Great Bustard life history estimates

Great Bustard Literature Review Life Table. March 2009				
Parameter	**Value (±SD)**	**Notes**	**Notes**	**Reference**
Age females first breed	2/3 years old			Estimated J.C. Alonso and co-workersa (unpublished data)
Age of first successful reproduction	4.20 years (sd=± 1.48)	females become sexually mature at 2 years old		Morales et al., (2002)
Age males first breed	5/6 years old	although it is likely that few males can copulate successfully		Martin & Morales (2002), Lane & Alonso (2001)
Maximum age	30 years	estimated from a captive individual.		Gewalt (1959)
Maximum age of breeding	20 years	H.Litzbarski estimation		Streich et al., (2007)
Sex ratio (eggs laid)	1:1			
Sex ratio (adults)	Varies with age	Highly variable between leks		
Maximum clutch size	3			Martin & Morales (2002)
% females with clutch of 1 egg	15.70%	Spain		Derived from Farag´o (1992) in Lane & Alonso 2001
% females with clutch of 2 eggs	49.80%	Spain		Derived from Farag´o (1992) in Lane & Alonso 2001
% females with clutch of 3 eggs	10.50%	Spain		Derived from Farag´o (1992) in Lane & Alonso 2001
% females with clutch of 1 egg	3.30%	Russia	The proportion of 3 egg clutches decreased over the laying period	Watzke (2006)
% females with clutch of 2 eggs	70%	Russia		Watzke (2006)
% females with clutch of 3 eggs	26.70%	Russia		Watzke (2006)
% females which are nonbreeders	24.0 (± 12.5)			Alonso and Alonso (1990) ± VORTEX default value
both sexes, survival to approx. 2 months old	43%			Ena et al. (1987)
both sexes, survival to approx. 2 months old	27%			Magana 2007(PhD thesis)
both sexes, survival to approx. 3-5 monthsold	30%			Martin et al., (2007)
both sexes, survival to 1 year	10%	interpolation of above 3 estimates		Martin et al., (2007)
% mortality both sexes 1-2 year	9.8%	Spain no SD reported		Martin et al., (2007)
% mortality both sexes >2 year	9.1(±1.6) %	Spain		Martin et al., (2007)
% mortality females 0–1 year	69.6 - 92.6 % (±6.28)			Alonso et al 2004
% mortality females 0-1 year	89.4% (±6.28)			Lane and Alonso 2001
% mortality females >1 year	7.5 %(± 11.81)			Derived from J.C. Alonso and co-workersa (unpublished data)
% mortality males 0–1 year	77.1 - 94.7 %(±6.36)			Alonso et al 2004
% mortality males 0-1 year	92.1 % (± 6.36)			Lane and Alonso 2001
% mortality males >1 year	13.3 % (± 12.0)			Derived from J.C. Alonso and co-workersa (unpublished data)
Survival Captive birds, from release to next spring	40% (range 17%-75%)			Eisenberg 2008
Productivity (chicks/female)	0.25 (range 0.24-0.27)	Russia 1999	Mean from two areas, showing variation in productivity	Watzke (2007)
Productivity	0.43 (range 0.41-0.49)	Russia 2000		Watzke (2007)
Productivity	0.24 ± 0.35 (range 0.00-3.00)	1 year	Spain	Martinez (2008)
Productivity	0.14 (range 0.04-0.29)	multiyear study	Spain	Morales et al., (2002)
Chance of breeding successfully 2 years in a row	14% of females successful 2 years in a row	mean across age classes, it increases with age	Spain	Morales et al., (2002)
% adults males in breeding pool	33%	from J.C. Alonso unpublished data. Consistent with other lekking species.		Lane and Alonso (2001)
Emigration rate	0 - 1.00	reflects an individuals choice to disperse		Alonso et al., (2004)
Immigration rate	0 - 1.00			Alonso et al., (2004)
% juvenile females dispersing	20%	Spain	median distance 18.1km (range 4.97-178.42 km)	Martin et al., (2008)
% juvenile males dispersing	75.60%	Spain	median distance 18.1km (range 4.97-178.42 km)	Martin et al., (2008)

One very long term study has drawn some very interesting conclusions from the dispersal patterns in the Spanish Great Bustard. Natal dispersal occurs in approximately 50% of individuals after which they take up residency at their definitive lek (Alonso et al. 1998). Most importantly the sexes display different dispersal tendencies, with 80% of females remaining faithful to their natal site as opposed to 75% of males dispersing from their natal site. Males are also found on average to disperse farther than females (Alonso & Alonso 1992; Martin et al. 2002) with a median dispersal distance of 18.1km (range 4.97-178.42 km) (Martin et al. 2008). It is not known why males disperse and the females remain philopatric. It could be partly driven by highly skewed reproductive success of a few individual males and thus to decrease the competition with his own offspring. On an individual level, not taking sex into account, Martin et al. (2008) identified two factors influencing an individual's choice to disperse. Isolated leks had a decreased chance of individuals dispersing, and individuals that did disperse showed longer dispersal distances than average. The size of the natal lek was also important to the probability of dispersing, the relationship being negatively correlated with individuals more likely to disperse from smaller leks. Referring to the habitat issues earlier, Great Bustards may not be sampling or assessing the quality of the habitat around them but rather using the presence of conspecifics as a measure of habitat quality (Alonso et al. 2004).

Although it is thought that Great Bustards remain faithful to a lek for their life, there is little data on the rate of dispersal in older birds, for example, do birds change their lek, disperse as they get older? There is some evidence to suggest that this is possible as the over twenty years of study in Spain and Portugal, they suggest that some leks have disappeared, big leks have been growing and smaller leks are getting smaller. The growth rate of these leks is only possible with immigration and birth. Great Bustards are also thought to live to thirty years old, so presumably birds do abandon leks and emigrate. Alonso et al. (2004) also quotes unpublished data to show that adult Great Bustards sometimes perform breeding dispersal.

Natal philopatry of females and dispersal of males could be driving genetic structures within populations. As found in the analysis of mitochondrial DNA (mtDNA) from Great Bustards at different breeding groups found sex differences in genetic structure. The female haplotypes divided up into three structured batches that were each separated by *ca.* 50km, where as male haplotypes were randomly distributed between the leks which is concordant with observational studies (Martin et al. 2002). These results suggest that isolation-by-distance can influence the distribution of maternal lineages at a regional level. Males dispersed to non-genetically similar groups. However, the use of one maternal marker for these studies is biased towards females, and where many genetic studies come from the analysis of chick blood, sampling the chicks before they leave means that only the maternal structure is

sampled. mtDNA is not the appropriate genetic marker for understanding the structure of male population the male's potential role in maintaining DNA variability (Martin et al. 2002; Martin et al. 2008). This has important implications of the wider conservation efforts of the species as understand the population structure of only the female population will lead to misconceptions about the population structure and evolutionary significant units. It is vital that when carrying out a population genetic structure analysis that the most appropriate genetic markers are chosen.

Migration

Great Bustards display different migration patterns across their range, sedentary in the west and migrants in the east. In Spain Great Bustards are classified as partial migrants with the different behaviour between the sexes. Radio-tracked females were found to have four different strategies, migration between breeding and wintering areas; only leaving their home-range to mate; migrating from wintering-breeding area to summer nesting area; and females that stayed all year round with a relatively small home-range (Alonso et al. 2000). Males were found to have two strategies; sedentary males that stayed within 2 to 3 km of their lek all year and migrants which moved between 7 and 20 km to post-breeding areas (Morales et al. 2000). The males consistently return to their lek and post-breeding areas. Their travel time was consistent between years but varied between individuals.

In Germany and Hungary, Great Bustards are known to be facultative migrants with the reported trigger thought to be depth of snow rather than temperature (Streich et al. 2006). This is also thought that males are less likely to migrate than females due to their size and weight. The migration pathways of German and Hungarian birds are much longer than those reported in Spanish birds, undertaking movements of greater than 1000 km during migration (Fig. 1, Streich et al. 2006). Although only a small proportion of this data was from marked individuals and the rest inferred through the timing of seasonal population declines and increases.

In Russia, Saratov females were marked and found to migrate over 1000 km to southern Ukraine in the winter (Watzke 2007b). Males were not marked and there is no data on the movements of males post-breeding in this population. However, in Ukraine it is estimated that 7,000- 8,000 Great Bustards regularly winter there potentially making it the most important Great Bustard wintering ground (Andryushchenko 2007). It is assumed that the majority of birds from Saratov migrate to Ukraine although this has never been confirmed with a large number of marked birds. Some migrants may come from other parts of Russia (e.g. Samara and Rostov oblasts) as well as western Kazakhstan.

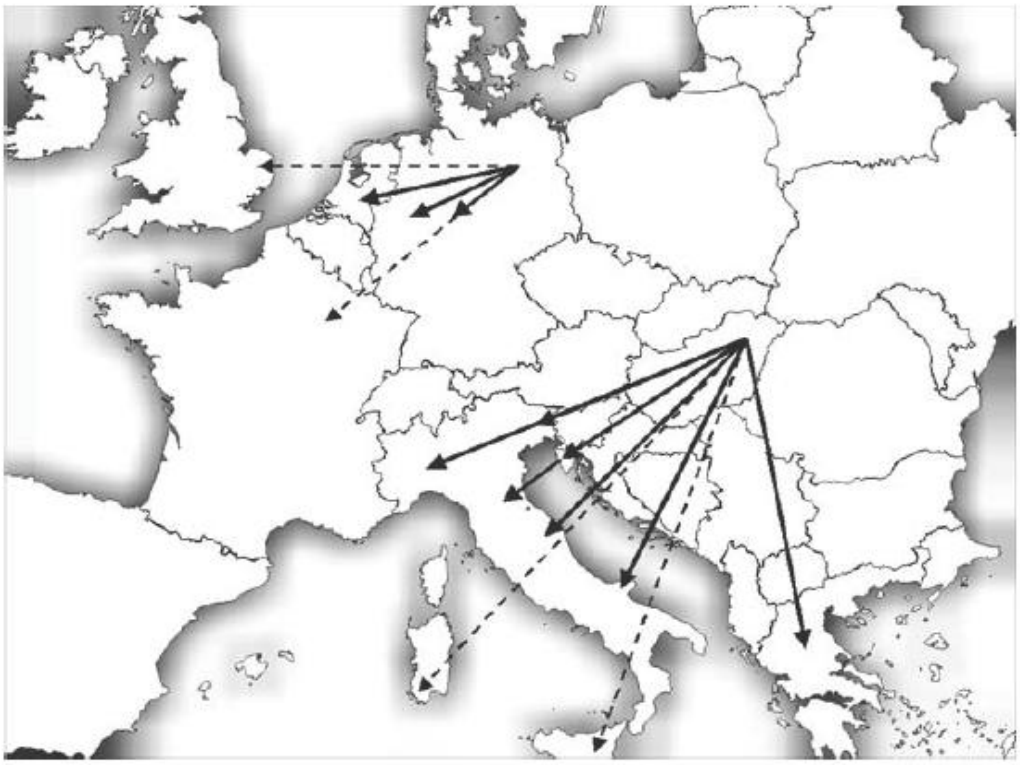

Figure 1. Great Bustard migration movements for Hungary and Germany. Taken from (Streich et al. 2006).

Productivity

It is difficult to study the productivity of Great Bustards due to their cryptic nature, i.e. difficult to observe copulations, find nests, observe chicks and mark the birds. Few studies have produced detailed estimates of Great Bustards (Morales et al. 2002). However, there some have produced single year estimates of productivity, i.e. the number of chicks surviving to December divided by the number of females, (Ena et al. 1987; Martinez 2008; Watzke 2007a). However, they are not able to quantify the individual variation in reproductive success between years. Identifying these parameters and more importantly the variation is important to the management of Great Bustard populations as it is a critical parameter in the persistence of populations (Morales et al. 2002). It provides a basis for modelling and designating benchmarks for population assessments.

From an 8 year study, Morales et al. (2002) found that productivity was low over all, with an average of 0.14 chicks per female, but the inter-annual variation was high (0.04-0.29). The only

significant abiotic predictor was a positive correlation with annual winter precipitation, dry winters resulting in low productivity. Two important results to come from this are: 1) the implication of maternal care that the chance of reproductive success improved with age. Although females become sexually mature at 2 years old, the mean first age of successful reproduction was 4.20 years (SD = ± 1.48). 2) And that the percentage of females able to breed successfully two years in a row was low (14 %) revealing possible heavy costs of maternal care. The chance of reproductive success also increased in females > 6 years from 0.20 to 0.40 (Morales et al. 2002). The average productivity in the study region Wildlife Reserve Villafalia, which is the densest breeding population in the world, had a lower productivity indicating that the area may be close to its carrying capacity.

Martinez (2008) also found an effect of density on productivity (0.24 ± 0.35) (range 0 - 3.0) during a single year study, comparing different leks**.** Productivity was negatively correlated with density suggesting again that density dependence can play a role in Great Bustard population dynamics.

From these estimates, we can see that there is on average low productivity across different study populations suggesting that low reproductive rates may be a part of the Great Bustard life history (Morales et al. 2002). The variance, when estimated was very large and population viability analysis indicts that the range of this variance can have important implications for the probability of extinction (Alonso et al. 2004; Lane & Alonso 2001; Pinto et al. 2005; Streich et al. 2007).

Survival and mortality

It is essential for population management to have an understanding of survival rates in threatened species. Due to the lack of long-term individual studies on Great Bustards there is little knowledge on the mortality rates. Survival is different between individuals and throughout various life stages; pre and post-fledging and adulthood. In the absence of reliable data, authors can sometimes utilise estimates from populations, such as Streich et al. (2007) using a first year mortality rate of approximately 20%, and Osborne (2005) using a first year survival rate of 88% for chicks. However, more reliable estimates from marked population have indicated that first year survival is likely to be much lower than the estimates used in these models. Utilisation of unconfirmed parameters can lead to mismanagement of a population through poor measures of performance.

Pre and post-fledging

Pre and post-fledging is the period of highest mortality in Great Bustards and can have important consequences for population persistence through recruitment. Until recently there has been only poor data available on the survival rate of chicks through their first year (Martin et al. 2007; Osborne 2005). Ena et al. (1987) found from one site, from one year that survival was 43% from hatching (May & June) to August (approx. 2 months old). Magana (2007) found survival rate from hatching in May/June to marking (late July) was 27% (approx. 2 months old). Martin et al. (2007) found that between survival between marking (2^{nd} half of July) and end of the summer was 0.30 (3-5 months old). From these three survival rates Martin et al. (2007) extrapolated a first year survival rate of 0.10. This suggests that survival rates are very low in a Great Bustard's early life and the majority of the mortality takes place in the first three months of a chick's life when it is most vulnerable. Due to small data sets and the necessity of averaging between, there is little understanding of the variation in the mortality rates, although it can be inferred that variation is important as indicated by varying levels in productivity.

Individual chick mortality was found to be influenced by maternal age as older females were more successful at rearing chicks than younger females (Morales et al. 2002; Morales & Martin 2002). This suggests that maternal experience may be important and this may be due to older mothers laying earlier (Martin et al. 2007). Martin et al. (2007) argues that this may explain the significant positive correlation between body mass at tagging and survival, because early chicks have a longer period to attain weight before food availability reduces as the season develops. When controlling for body weight, it was found that males have a higher mortality rate than females in their first few months possibly caused by a male's greater need for resources. Male chicks grow faster than females and are already noticeably larger after a couple of months (Alonso et al. 1998; Martin et al. 2007).

Captive reared Great Bustards

It is questionable how wild reared chick mortality rates can be applied to captive reared (CR) chicks as CR birds skip the first three months of mortality risks wild birds are exposed to. CR birds are approximately 3 months old when released and theoretically should have a lower mortality rate but it is generally found that captive reared birds are less able to survive in the wild than their wild counterparts.

Techniques of raising Great Bustards in captivity to release have been improved over the past couple of decades. Captive rearing programs in Germany and the UK have both shown low pre-release

mortality rates (pers comm. D Waters (Langgemach 2008). However, post-release mortality rates have often been thought of as high. Mortality rates for captive reared bustards in Germany surviving from autumn to the next spring is between 30-40% although the range of 20 - 75% survival (Eisenberg 2008). Monitoring of mortality after this initial period in Germany has been inadequate to produce reliable adult mortality rates.

Adult survival

There is little to no published data on adult survival rates, and they can only be reliably estimated with a reasonable sample size from marked individuals. However the estimates of survival from the second year to first year of breeding are 90 % (Martin et al. 2007). These have been estimated for the marked Spanish population from unpublished data. This is consistent with the longevity and large size of the Great Bustard (Alonso et al. 2004; Lane & Alonso 2001).

Longevity estimates are also unreliable as currently Great Bustards are estimated at to live to 30 years based on the age of captive birds but I am not aware of any study that has had a marked individual in the wild for such a long period of time. Realistically, the birds are unlikely to live this long in the wild, especially with modern threats. A simple calculation of survivorship to 30 years from age 1 at an annual mortality rate of 0.9 tells us about 4% of individuals could reach this age. Even if a bird reaches this age they may have lost the ability to be a successful reproducer. H. Litzbarski estimated the maximum breeding age of Great Bustards as 20 years old (Streich et al. 2007). However, there is still no quantitative evidence for this. Final age of breeding may be a more applicable population management parameter than longevity.

Population survival

Population viability analysis (PVA) is a useful analysis to carry out to learn what parameters may be important in determining the chance of extinction. It can allow us to understand how a set of complex parameters interact and we can create some threshold values as indicators of population health. There have four PVAs published on local Great Bustard population, all reaching similar conclusions about the parameters the model is sensitive to, namely: female productivity and female survival.

Streich et al. (2007) estimated very low mortality rates for first year juveniles (0.20). However, the model was still sensitive to female productivity and female survival. Using higher chick juvenile

mortality rates (~0.90), Pinto et al. (2005) and Lane & Alonso (2001) found similar sensitivity in their PVAs. The critical values affect recruitment, but the effect of differential recruitment is sensitive to adult mortality rates. Because of this sensitivity the authors say that small improvements in these parameters can dramatically reduce the probability of extinction in individual leks. However, using actual values from these PVAs would be unadvisable because of the invalidity of some of the life history parameters. The models which have many validated parameters fail to incorporate immigration and emigration which may play a significant role in the probability of extinction due to the meta-population nature of regional Great Bustard populations (Alonso et al. 2004; Lane & Alonso 2001; Pinto et al. 2005). Alonso et al. (2004) took the importance of juvenile dispersal into account in the most recent model, validating the model with real census data on several leks. Without dispersal taken into account, the model was a poor reflection of the real data.

Another parameter that has been found to influence population persistence is initial population size. Authors have noted that there are important threshold values that can be applied to natural breeding populations. Alonso et al. (2004) noted in a study that big leks had a tendency to increase, were as small leks had a tendency to decrease. In this ten year study, the largest initial population was 91 and the smallest was 34, and taking conspecific attraction into account, lek size should be a relative term. Notably in this study none of the leks had fewer than 30 individuals and none went extinct. Pinto et al. (2005) found from actual long term census data that leks below the size of 30 birds had a much higher risk of extinction, with seven leks from the study going extinct and three following decreasing trends. Whether a lek goes extinct through the process of death or from breeding dispersal is unclear, but the leks that went extinct held below 10 individuals. Small populations are always at risk of extinction through demographic stochasticity, and inbreeding depression. Isolated populations also fall out of the metapopulation structure, decreasing the number of dispersers finding them through years of low recruitment. Isolation may increase the time, energy and mortality risks of its potential juvenile dispersers (Martin et al. 2008).

Threats

It is appropriate to discuss the threats to Great Bustard survival. Threats operate at several different levels which affect the birds at different times of their life. Firstly there is the indirect pressure to population through habitat degradation or loss, secondly the threat of having small fragmented populations, both of which have partially been covered earlier. Thirdly there is direct mortality to juveniles and adults.

As the bird ages, the cause of mortality skews from natural causes to non-natural causes (Martin et al. 2007). However, what becomes clear in the literature is that the great threats faced by Great Bustards are similar throughout its range. During early life, predation is the greatest threat, whereas the two most significant mortality threats for adults are power line collision and hunting.

Pre and post fledging chicks

Watzke (2007a) noted that farming practices are the main cause of loss of broods and chicks in the Saratov region, the sowing and cutting of winter and summer crops coincide with nesting periods and during chick development when they are unable to fly. The loss of clutches to predation from rooks and hooded crows was only noted if nests were disturbed by farming leading to a biased sample and estimates.

In Spain, it has been noted that a large proportion of chicks are predated (Martin et al. 2007). Starvation also causes mortality in chicks and it has been suggested this can be managed by a reversion back to low intensity farming which would increase food supplies for chicks (Lane & Alonso 2001).

In Hungary, the number one threat to Great Bustards is mammalian predators (Bankovics 2005). Predators are also the main threat faced by captive reared Great Bustards as to predation is the most significant cause of mortality in captive reared birds in the UK and Germany (Dawes 2008; Eisenberg 2008)

As the birds reach adulthood they are less susceptible to predation, but their size makes them a popular game bird to poach. This along with power lines are noted as the main causes of adult mortality in Russia (Watzke 2007a); Spain (Janss & Ferrer 2000; Martin et al. 2007); Hungary (Bankovics 2005); Austria and Morocco (Alonso et al. 2005b).

Genetics

To maximise the efficiency of conservation efforts, it is very important to understand the structure of a population and the diversity within it. Populations hold a varying degree of genetic uniqueness and it is important to conserve this diversity. Genetic analysis has lead to the study of phylogenetic structure, which is the genetic structure present within a population. If these units are different enough, populations can be split into evolutionary significant units (ESU). ESUs may have followed an independent recent evolutionary path and as such one unit may be better adapted to an environment

than another. It is recommended these units are managed separately to conserve the diversity within that particular species.

Pitra et al. (2000) quantified two Great Bustard ESUs from Iberia and central/eastern Europe with evidence of recurrent local evolution in the European populations (Table 3). Since this, several populations have been analysed at a regional scale to find micro structures within populations. These analyses have inferred population structure and gene flow between and within populations and sub-populations. Two significant findings from these studies are, 1) Spanish female philopatry has been strong enough to develop significant genetic population structure at a regional level of up to *ca.* 50km (Martin et al. 2002). 2) Studies on Russia/Ukrainian and Hungarian populations have revealed local evolution but with recurrent gene flow between the populations suggesting that female Great Bustard dispersal over large distances (Pitra et al. 2007) Szabo, pers. comm).

The possibility that females may be less philopatric outside of Spain has never been studied on marked wild populations from Europe. But they are known to undertake long migrations (see above section). Alonso et al. (2000) found that for the female partial migrants in Spain, individuals that had dispersed farther to settle at a lek where more likely to undertake a migration.

A problem with genetic studies on Great Bustards is they have been limited to mtDNA which is maternally inherited and therefore will only give an estimation of female structuring. It is evident from the study by Martin et al. (2002) that strong female philopatry may enhance mtDNA genetic differentiation allowing for less accurate inferences males population structure. The strong tendency of males to disperse may contribute to nuclear DNA diversity (Martin et al. 2002). Where possible, genetic structures should also be confirmed through the analysis of nuclear DNA (Alonso et al. 2008; Lieckfeldt et al. 2001).

Table 1 Geographic distribution of mtDNA haplotypes*; nucleotide diversity (π), haplotype diversity (δ), and average number of nucleotide differences (k) within great bustard populations in Europe. Unshaded and shaded rows represent haplotypes observed in either the European mainland or the Iberian Peninsula, respectively

Haplotypes	variable sites† 11111 56666 566781223 736688000 479381495	Madrid 40°31′ N 3°35′ W Spain	Cáceres 39°34′ N 6°32′ W Spain	Rathenow 52°39′ N 12°20′ E Germany	Dévaványa 47°4′ N 20°59′ E Hungary	Nitra 48°23′ N 18°8′ E Slovakia	Saratov 51°39′ N 45°57′ E Russia	Number of individuals
A	CGATGCGAT	5	4					9
B	TA.....		3					3
C	TA A....	16						16
D	..G.....	4	2					6
E	.....AG.			11	5	3	5	24
F	T.....AG.					2		2
G	..G...AG.				2			2
H	.......G.					1		1
I	T..G.TA..						1	1
J	..G...AGA						1	1
K	T....TA..						1	1
number of individuals		25	9	11	7	6	8	Σ = 66
π (%)		0.21	0.17	0.00	0.06	0.11	0.25	
δ		0.55	0.59	0.00	0.48	0.73	0.50	
k		1.72	1.39	0.00	0.48	0.87	2.04	

*Numbers in location columns represent occurrences and their totals, and the rightmost column shows total occurrences for each haplotype. †Nucleotide position numbers of the great bustard mtDNA correspond to positions in the complete *Vidua chalybeata* mtDNA genome (AF090341). Dots indicate identity with the reference sequence (haplotype A), and letters designate base substitutions.

Table 3. Mitachondrial haplotypes of six national breeding Great Bustard populations. Taken from (Pitra et al. 2000).

Conservation

The recent Memorandum of Understanding meeting in 2008 phrased it well; "*The level of research is still inadequate to provide solid science basis for conservation measures*" (CoMS 2008). This is true for the central and eastern European populations of Great Bustard. However, there is a growing amount of scientific work on the Spanish population leading to informed decisions about the management strategies based on the species biology. The studies of the Iberian populations highlights the difficulties in monitoring populations of Great Bustards which has ultimately taken them 30 years to develop the correct techniques. By far the greatest advancement in their research has been through radio-tagging individual birds.

Historically, the European population would have had a distribution across all of central Europe, Eastern Europe, Russia, Asia and north Africa. These populations could have potentially had the ability to remain connected through a stepping stone meta-population structure. Iberian population has shown that meta-population structure is functioning with a high variance in productivity between leks and that immigration and emigration can affect the probability of extinction for a lek (Alonso et al. 2004). Maintaining a lek is very important as the bustards show an extremely low ability to colonise new areas and that conspecific attraction may be the over-riding force in decisions to disperse or stay. This new understanding of the metapopulation and lek fidelity of the Great Bustard may give us insight into why it was vulnerable to such wide spread decline in Europe.

Lessons on the Great Bustard's behavioural biology could help inform further initiatives for reintroduction and supplementation projects.

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